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Title: The use of biogeochemical models to evaluate mitigation of
greenhouse gas emissions from managed grasslands

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Keywords: GHG emission intensity, livestock density; nitrogen
fertilization, process-based model, sensitivity analysis

Corresponding Author: Dr. Gianni Bellocchi, PhD

Corresponding Author's Institution: French National Institute for
Agricultural Research

First Author: Renáta Sándor

Order of Authors: Renáta Sándor; Fiona Ehrhardt; Lorenzo Brilli; Marco
Carozzi; Sylvie Recous; Pete Smith; Val Snow; Jean-François Soussana;
Christopher D Dorich; Kathrin Fuchs; Nuala Fitton; Kate Gongadze; Katja
Klumpp; Mark Liebig; Raphael Martin; Lutz Merbold; Paul C.D. Newton;
Robert M Rees; Susanne Rolinski; Gianni Bellocchi, PhD

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also in combination with decreasing N fertilisation levels (reduced to
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Abstract

Simulation models quantify the impacts on carbon (C) and nitrogen (N) cycling in grassland systems caused by changes in management practices. To support agricultural policies, it is however important to contrast the responses of alternative models, which can differ greatly in their treatment of key processes and in their response to management. We applied eight biogeochemical models at five grassland sites (in France, New Zealand, Switzerland, United Kingdom and United States) to compare the sensitivity of modelled C and N fluxes to changes in the density of grazing animals (from 100% to 50% of the original livestock densities), also in combination with decreasing N fertilisation levels (reduced to zero from the initial levels). Simulated multi-model median values indicated that input reduction would lead to an increase in the C sink strength (negative net ecosystem C exchange) in intensive grazing systems: - $64 \pm 74 \text{ g C m}^{-2} \text{ yr}^{-1}$ (animal density reduction) and $-81 \pm 74 \text{ g C m}^{-2} \text{ yr}^{-1}$ (N and animal density reduction), against the baseline of $-30.5 \pm 69.5 \text{ g C m}^{-2} \text{ yr}^{-1}$ (LSU [livestock units] $\geq 0.76 \text{ ha}^{-1} \text{ yr}^{-1}$). Simulations also indicated a strong effect of N fertilizer reduction on N fluxes, e.g. N_2O -N emissions decreased from 0.34 ± 0.22 (baseline) to $0.1 \pm 0.05 \text{ g N m}^{-2} \text{ yr}^{-1}$ (no N fertilization). Simulated decline in grazing intensity had only limited impact on the N balance. The simulated pattern of enteric methane emissions was dominated by high model-to-model variability. The reduction in simulated offtake (animal intake + cut biomass) led to a doubling in net primary production per animal (increased by $11.6 \pm 8.1 \text{ t C LSU}^{-1} \text{ yr}^{-1}$ across sites). The highest N_2O -N intensities (N_2O -N / offtake) were simulated at mown and extensively grazed arid sites. We show the possibility of using grassland models to determine sound mitigation practices while quantifying the uncertainties associated with the simulated outputs.

Keywords: GHG emission intensity, livestock density; nitrogen fertilization, process-based model, sensitivity analysis

1. Introduction

Finding solutions to emerging ecological and societal challenges (climate change, food security, ecosystem sustainability) requires improved knowledge of the underlying processes affecting carbon-nitrogen (C-N) pools and fluxes in agricultural systems (West et al., 2002; Giardina et al., 2014; Campbell and Paustian, 2015). Grassland ecosystems have a potentially important role to play in meeting the challenge of climate change because they can act as a source or sink for atmospheric carbon dioxide (CO₂) (Smith et al., 2008; Oates and Jackson, 2014) and are a source of non-CO₂ greenhouse gases (GHG) such as nitrous oxide (N₂O) and methane (CH₄). Importantly, these GHG emissions can be manipulated by management such as the method of grazing and the fertiliser regime (Soussana et al., 2004; Herrero et al., 2016). Several grassland experiments have addressed the role of management on the short-term GHG balance and global warming potential (e.g. Allard et al., 2007; Soussana et al., 2007; Hörtnagl et al., 2018). However, direct measurement of C-N balances should be supplemented by the use of simulation models, to support the implementation of effective practices and policies in agriculture, e.g. to mitigate GHG emissions (Rosenzweig et al., 2014; Elliott et al., 2015; Folberth et al., 2016). Biogeochemical process models address many of the complex interactions of weather, soil, vegetation and management practices (Bondeau et al., 1999; Churkina et al., 1999; Huntzinger et al., 2012; Warszawski et al., 2014; Chang et al., 2015) and can do so over long time intervals that are not feasible with experimentation. Existing modelling studies have focused on the determination of the C source and sink activity of grasslands (Soussana et al., 2010). Grassland models have been shown to provide adequate accuracy in representing observed yield and GHG emissions across a wide range of environments and management intensities (e.g. White et al., 2008; Chang et al., 2013; Graux et al., 2013; Ben Touhami and Bellocchi, 2015; Ma et al., 2015; Senapati et al., 2016; Ehrhardt et al., 2018).

Models can thus be beneficial for decision makers and farmers because they can be used to explore the productivity and environmental performances of specific systems as a consequence of changed management. However, the effect of management on C and N fluxes in agriculturally managed permanent grasslands (not re-sown more frequently than every five years, which is the focus of this study) is often uncertain (Schulze et al., 2009; Ciais et al., 2010), and such uncertainties are reflected in the outputs of the models used to simulate responses to management (Sándor et al., 2017). Grasslands are highly complex ecosystems and their behaviour is affected by multifaceted interactions of management drivers with water and nutrient availability, soil physics, and vegetation dynamics (Rees et al. 2013; Soussana et al., 2013). The dynamic grassland simulation models developed since the 1990s (e.g. Challinor et al., 2013; Snow et al., 2014; Calanca et al., 2016; Jones et al., 2017a) differ greatly in their treatment of key processes, and hence in their response to environmental and management conditions (Brilli et al., 2017). A thorough assessment of the variation in the response, or sensitivity, of different grassland models to management factors can be critical in determining to what extent simulated responses may vary depending on the model used. From a policy perspective, it is critically important to identify the extent to which management interventions influence C-N fluxes (including productivity) prior to promoting policies that alter farming practices. If the impact of a given practice is uncertain, a sensitivity analysis can give information on the reliability of the models when representing C-N fluxes-management relationships under a variety of conditions. It is thus important to examine model behaviour under changed management in order to characterise the types of responses estimated, contrast the responses of different models and consider the reasons for these differences. In particular, hypotheses about the contribution of grassland management to GHG emissions can be tested *via* simulation models, which allow understanding, diagnosing and forecasting complex

interactions (Chen et al., 2008; Seijan et al., 2011; Graux et al., 2012; Sándor et al., 2017, 2018).

Consequently, using five case studies, we tested the sensitivity of eight grassland models to gradients of management intensity that were selected for their potential to mitigate GHG emissions (e.g. Soussana et al., 2014; Abdalla et al., 2017). With the aim of increasing the reliability and confidence in simulated results, a multi-model ensemble approach was adopted to explore patterns of simulated C and N responses against imposed gradients of N fertilisation and animal stocking rate (to which grassland models are generally sensitive, after Brilli et al., 2017). For this study, we included a range of well-known grassland models, and used them to simulate biogeochemical and related outputs (productivity and energy measures). The wider ensemble analysis presented in Ehrhardt et al. (2018) forms the baseline for the work presented here, which analyses factors that may explain the major differences observed in model responses. We further explored to what extent multi-model ensembles can be used to help identify farming practices that reduce GHG emissions. While restricting the analysis to a limited set of management options, this study examines a wide range of output variables and thus provides a framework for assessing grassland performance where direct casual links with farming practices are not obvious, and changes in performance are difficult to measure. As a corollary outcome, viewing and interpreting a variety of model outputs lay ground for future model developments.

2. Materials and Methods

We refer to a sub-set of the grassland models described in Ehrhardt et al. (2018), in which models were initialized and calibrated using vegetation and soil variables, and surface-to-atmosphere fluxes at four sites worldwide. We used an ensemble of grassland models (Table 1) and compared their sensitivity to changes in management by comparing simulated

100 outputs against gradients of management practices. Model anonymity was maintained
101 throughout the process and model results are presented without attributing them to specific
102 models or modelling teams.

103

104 Table 1. The biogeochemical models used for testing the impact of grassland management
 105 options.

Model / Version	Description / References
APSIM-SWIM v7.7	APSIM (The Agricultural Production Systems sIMulator; Holzworth et al., 2014) simulates several systems through the interaction among plants, animals, soil, climate and management. The model allows the analysis of the whole-farm system, including livestock, crop and pasture sequences and rotations. Users can select between two soil water models: the capacitance-based SoilWater (Probert et al., 1998) and SWIM, which is based on Richards' equation (Huth et al., 2012). The pasture model was that of Li et al. (2011).
APSIM-SoilWater v7.7	
DayCent v4.5 2006	DayCent is the daily time-step adaptation of the biogeochemical model CENTURY (Parton et al., 1998). It simulates biomass growth, soil C dynamics, N leaching, gaseous emissions (e.g. N ₂ O, NO, N ₂ , NH ₃ , CH ₄ and CO ₂) and C fluxes (e.g. NPP, NEE) in croplands, grasslands, forests and savannahs, as affected by management practices (such as fertilization, tillage, pruning, cutting and grazing) and specific external disturbances (e.g. fires). Different versions of the model result in different parameter settings and a few variations in the model structure. DayCent v4.5 2006 applies grazing on a daily basis as linear impact on aboveground biomass and root/shoot ratio, with aboveground biomass removed as a percentage of total aboveground biomass. DayCent v4.5 2010 and 2013 apply grazing on a daily basis with aboveground biomass removed as a percentage of total aboveground biomass rather than as continuous grazing. In DayCent models after 2013, water stress effect on biomass production differs from the previous versions.
DayCent v4.5 2010	
DayCent v4.5 2013	
LPJmL v.3.5.003	LPJmL (Lund-Potsdam-Jena managed Land) explicitly simulates key ecosystem processes such as photosynthesis, plant and soil respiration, C allocation, evapotranspiration and phenology of nine plant functional types representing natural vegetation at the level of biomes (Sitch et al., 2003), and of 12 plant functional types (Bondeau et al., 2007; Rolinski et al., 2018).
PaSim	PaSim (Pasture Simulation model; Riedo et al., 1998; Calanca et al., 2007; Ma et al., 2015) is a process-based, grassland-specific ecosystem model that simulates grassland productivity and GHG emissions to the atmosphere. The model consists of sub-models for vegetation, grazing animals, microclimate, soil biology, soil physics and management.
SPACSYS v5.0	SPACSYS (Wu et al., 2007, 2015) is a multi-layer, field scale, weather-driven and daily-time-step dynamic simulation model. The current version includes a generic plant growth and development, C and N cycling, plus simulation of soil water that includes representation of water flow to field drains as well as downwards through the soil layers, together with a heat transfer component. The model simulates root architecture.

We present multi-model medians and box-plots, and focus on long-term averages for the same four grassland sites (G1 to G4) described in Ehrhardt et al. (2018) plus an additional site (G5) for which full calibration was only completed after the initial publication (Table 2). Overall, there is a lack of case studies in Asia, Africa and South America (which would have extended the comprehensiveness of the research), but sites from G1 to G5 are intended to represent situations commonly encountered in temperate grasslands. While the choices made are described in Ehrhardt et al. (2018), in summary it was thanks to international collaborations that we could pool and share experimental data for five grassland sites (one more than in Ehrhardt et al., 2018). These sites provided high- quality, previously published data encompassing climate, soil, agricultural practices, and C and N fluxes.

Table 2. Selected grassland sites for the modelling exercise.

General description		Grassland sites				
Site code		G1	G2	G3	G4	G5
Country		United States	New Zealand	France	United Kingdom	Switzerland
Location		Mandan	Flockhouse	Laqueuille	Easter Bush	Chamau
Climate ¹		Dfb (humid continental)	Cfb (oceanic)	Cfb (oceanic)	Cfb (oceanic)	Cfb (oceanic)
Latitude		46.77	-40.20	45.64	55.52	47.20
Longitude		-100.89	175.30	2.74	-3.33	8.40
Elevation a.s.l. (m)		591	30	1040	190	393
Simulation period		2003-2006	1997-2008	2003-2012	2002-2010	2010-2013
Mean annual minimal air temperature (°C) ²		0.0±1.0	9.1±0.5	4.0±0.6	4.6±0.9	4.4±0.6
Mean annual maximal air temperature (°C) ²		11.9±1.3	17.6±0.6	11.0±0.8	11.4±0.8	14.7±0.8
Mean annual cumulated precipitation (mm) ²		411±128	896±107	1047±144	961±142	1084±143
Management						
Type		Grazed	Grazed	Grazed	Grazed / mown	Grazed / mown
Animal type		Yearling steers	Non-lactating sheep	Heifers	Ewes, lambs, heifers and calves	Sheep
Mean annual number of grazing days ³		107	22	163	162	14
Stocking rate (LSU ha ⁻¹ yr ⁻¹) ³		0.08	1.29	1.34	0.76	0.10
Vegetation type		C3 grasses	C3 grasses,	C3 grasses,	C3 grasses	C3 grasses,

		legumes, forbs, C4 grasses	legumes, forbs		legumes
Mean annual number of cutting events ³	0	0	0	0.9	6.3
Total annual N fertilisation (kg N ha ⁻¹ yr ⁻¹) ³	0	0	210	220	230
Soil properties					
Soil type ⁴	Calcic Siltic Chernozem	Mollic Umbrisol	Loamic Andosol	Eutric Cambisol	Gleysol
Maximum depth of the soil profile (m)	4	0.9	0.9	1.0	1.0
Number of documented layers	6	4	5	5	4
Soil texture: ~sand (%) ⁵	29.7	93.1	24.6	22.9	57.2
~silt (%) ⁵	51.0	3.8	55.5	19.0	28.9
~clay (%) ⁵	19.5	3.1	21.8	58.1	14.0
Bulk density (gcm ⁻³) ⁵	1.17	1.20	0.67	1.45	1.34
References	Liebig et al. (2006, 2010, 2013)	Newton et al. (2010, 2014)	Allard et al. (2007); Klumpp et al. (2011)	Skiba et al. (2013); Jones et al. (2017b)	Imer et al. (2013); Merbold et al. (2014)

¹Köppen-Geiger climate classification (Kottek et al., 2006).

²Mean minimum and maximum air temperatures, and precipitation totals calculated over 30 years (1980-2009) using AgMERRA (<https://data.giss.nasa.gov/impacts/agmipcf/agmerra>) meteorological datasets (Ruane et al., 2015).

³Mean values over the simulation period. Grazing at G2 site was on a rotational basis, i.e. animals were brought in at intervals for short periods at a high stocking rate, while at all other sites grazing was by set-stocking, i.e. animals were maintained continuously on the pasture at a low stocking rate.

⁴World Reference Base for Soil Resources (FAO, 2014).

⁵Mean values across multiple layers.

To analyse the sensitivity of models with respect to changes in grassland management practices, viz. animal stocking density and N fertilisation, management scenarios were obtained by adjusting the observed baseline management (business-as-usual) for each site with systematic decrements over a range of values (Table 3). Sensitivity is defined as the proportional change in models outputs that results from a change in a given factor (here management practices).

In our study-sites, two major practices are responsible for C and N fluxes from grasslands: (1) vegetation removal and (2) fertilizer inputs. The harvesting of vegetation was predominantly controlled by grazing animals for the majority of sites. The exception was G5 where the grazing was light and vegetation was predominantly removed by cutting. Accordingly, a reduction in grassland use was assessed by a limitation of livestock density,

either alone or together with reduction (down to cessation) of fertilizer N in N-fertilised sites (G3, G4 and G5) (Table 3). The livestock unit (LSU) based on the grazing equivalent of one adult cow was used to compare different animal types (yearling steers, non-lactating sheep, ewes, lambs, heifers and calves).

Table 3. Design of management options (where 100% indicates the baseline - business-as-usual - management scenario).

Action ¹	Sites	Description
Reduction of livestock density (LD)	G1, G2, G3, G4, G5	The livestock density in the pasture was decreased in five steps of 10% (from 100% down to 50% of the livestock density indicated by the default standard management)
Abbreviations ² : LD ₉₀ , LD ₈₀ , LD ₇₀ , LD ₆₀ , LD ₅₀		
Reduction of livestock density (LD) and nitrogen (N) fertilizer	G3, G4, G5	The amount of mineral or slurry N added to the pasture was decreased in five steps of 20% (from 100% to 0% of the N amount indicated by the default standard management), whilst the livestock density in the pasture is decreased in five steps of 10% (from 100% down to 50% of the livestock density indicated by the default standard management)
Abbreviations ² : LD ₉₀ N ₈₀ , LD ₈₀ N ₆₀ , LD ₇₀ N ₄₀ , LD ₆₀ N ₂₀ , LD ₅₀ N ₀		

¹When animal density was decreased, cutting events (if present) were left unaltered. When present, supplementary feeding was proportionally reduced along with the animal density.

²Percent livestock density (90, 80, 70, 60, 50) or N fertilizer (80, 60, 40, 20, 0) against baseline (business-as-usual). Without assessing all possible LD x N combinations, we focussed on reducing overall levels of management intensity through reductions in N inputs and grazing levels (according to most agri-environment schemes for grassland; Atkinson et al., 2005).

Impacts of the defined changes in management were calculated on the changes in a set of output variables related to biomass production and C-N fluxes (Table 4). Fluxes of CO₂ included emissions from ecosystem respiration (R_{ECO}), respiration from plants (R_{PLANT}), soil (R_{SOIL}) and grazing animals (R_{ANIMAL}) as well as estimates of the plant production of organic compounds from atmospheric CO₂ (GPP) and other system variables: Net Ecosystem Exchange, NEE=R_{ECO}-GPP; Net Primary Production, NPP=GPP-R_{PLANT}; Net Biome

Production, $NBP = -NEE + C$ losses through enteric CH_4 emissions at pasture, forage harvests and milk production at pasture.

Methane released from soil and enteric fermentation in animals was included in the list of non- CO_2 fluxes, along with the gaseous N compounds emitted to the atmosphere: N_2 (N gas), NO_x (N oxides: the sum of N monoxide, NO, and N dioxide, NO_2), N_2O (nitrous oxide) and NH_3 (ammonia). Nitrogen lost by nitrate (NO_3) leaching was also examined. The biological information included productivity measures such as the plant biomass produced above – and below-ground (AB and BB), two outputs of agronomic interest – the plant biomass consumed by grazing animals (Intake) or otherwise harvested (HAB), and their sum (Offtake) – and the energy that ultimately is utilised by grazing animals ($ME_{Offtake}$: offtake metabolisable energy).

To estimate the amount of plant biomass available for feeding animals, the annual NPP values were normalized by animal stocking rates. We also expressed C and N fluxes relative to the overall productivity of the system, so that we could express the intensity of GHG emissions on the basis of productivity (i.e. g of emitted C or N per g C of harvested or per g C ingested dry matter, DM). This approach is similar to the concept of ‘yield-scaled emission’ or emissions intensity as defined by Van Groenigen et al. (2010) and has important policy significance and delivers results that are relevant to stakeholders (Venterea et al, 2011; Valin et al., 2013). For this purpose, three additional variables were analysed, representing the ratios of CO_2 -C, N_2O -N and CH_4 -C emissions to the total amount of C biomass (Offtake) consumed by animals (Intake) and harvested as fodder (HAB): $Int_{CO_2-C} = -NEE/Offtake$, $Int_{N_2O-N} = N_2O-N/Offtake$, $Int_{CH_4-C} = CH_4-C/Offtake$.

183 Table 4. Model outputs (annual cumulative) generated by each model (✓: available; NA: not
184 available) and assessed in the study. The identities of models were kept anonymous by using
185 the same model codes as in Ehrhardt et al. (2018).

Variable/Models			M05	M06	M07	M08	M16	M22	M24	M28
CO ₂ fluxes	GPP (gross primary production): g C m ⁻²		✓	✓	✓	✓	✓	✓	✓	✓
	NPP (net primary production): g C m ⁻²		✓	✓	✓	✓	✓	✓	✓	✓
	NEE (net ecosystem exchange): g C m ⁻²		✓	✓	✓	✓	✓	✓	✓	✓
	NBP (net biome production): g C m ⁻²		NA	✓	NA	NA	✓	NA	✓	✓
	R _{ECO} (ecosystem respiration): g C m ⁻²		✓	✓	✓	✓	✓	✓	✓	✓
	R _{PLANT} (plant respiration): g C m ⁻²		✓	✓	✓	✓	✓	✓	✓	✓
	R _{SOIL} (soil respiration): g C m ⁻²		✓	✓	NA	✓	✓	✓	✓	✓
	R _{ANIMAL} (animal respiration): g C m ⁻²		NA	✓	NA	NA	✓	NA	✓	NA
	CH ₄ emissions (methane) ² : g C m ⁻²		NA	✓	✓	✓	✓	NA	✓	NA
Non CO ₂ fluxes ¹	N ₂ O (nitrous oxide) emissions: g N m ⁻²		✓	✓	✓	✓	✓	NA	✓	✓
	NH ₃ (ammonia) emissions: g N m ⁻²		NA	✓	NA	✓	✓	NA	✓	NA
	NO _x (nitrogen oxides) emissions: g N m ⁻²		NA	NA	✓	✓	NA	NA	NA	NA
	N ₂ (nitrogen gas) emissions: g N m ⁻²		NA	✓	✓	✓	NA	NA	✓	✓
	N (nitrogen) leaching: g N m ⁻²		NA	✓	NA	✓	✓	NA	✓	✓
Productivity and energy	Aboveground (AB): g DM m ⁻²	biomass	NA	✓	✓	✓	✓	✓	✓	✓
	Belowground (BB): g DM m ⁻²	biomass	NA	✓	✓	✓	✓	NA	✓	✓

Harvested biomass (HAB): g DM m ⁻²	NA	✓	✓	✓	✓	NA	✓	✓
Animal intake (Intake): g DM m ⁻²	NA	✓	NA	✓	✓	✓	✓	✓
Metabolisable energy of Offtake (grazing plus harvesting) (ME _{Offtake}): MJ kg ⁻¹ DM	NA	✓	NA	NA	NA	NA	✓	NA

¹Fluxes are expressed in units of C (CH₄-C) and N (N₂O-N, etc.).

²CH₄ emissions include emissions from both animals (enteric) and their manure. The latter were estimated for M16, and the former were estimated for M06, M08 and M24; all estimations were based on Clark et al. (2003).

Following Sándor et al. (2016), we report the proportional change, named effect size of mean annual output variables from a change in each factor relative to the baseline management at each site.

The N₂O-N emission factor (EF) for fertiliser was calculated as percent ratio of the total yearly N₂O-N emissions over the amount of the annual N fertiliser. This simplified version of the N₂O-N emission factor calculation does not take into account of background emissions because not all the models allowed for a consistent estimation of this component. For this reason, following the IPCC (2006) guidelines, 1 kg N₂O-N ha⁻¹yr⁻¹ background emission was subtracted from the simulated values.

The present study was based on yearly aggregated model outputs. R software (R Core Team, 2016) was used for statistical computing and visualization. Accounting for the different global warming potential (GWP) of CO₂, CH₄ and N₂O, total GHG balances were achieved by converting CH₄ and N₂O emissions rates to CO₂ equivalents (CO₂e) using the 100-year Global Warming Potential (GWP₁₀₀) as established in national GHG inventories, i.e.: 1 kg N₂O=298 kg CO₂e, 1 kg CH₄=25 kg CO₂e (IPCC, 2006; <https://www.epa.gov/ghgemissions/understanding-global-warming-potentials>). Mass factors were also applied to model outputs, the latter being expressed in C and N units: 1 kg CH₄-C=1.33 kg CH₄, 1 kg N₂O-N=1.57 kg N₂O, 1 kg CO₂-C=3.67 kg CO₂.

3. Results and Discussion

Simulated results are presented and discussed separately, with selected graphs, for the following groups of variables: CO₂ fluxes, non-CO₂ fluxes, productivity and energy, and emission intensities. Additional results are provided in the supplementary material (Figs. A to S).

3.1. CO₂ fluxes

In the baseline scenario, GPP showed a wide range of variations in multi-model medians (137.2-1732.4 g C m⁻²), while animal respiration (R_{ANIMAL}) was the output with the least divergent results amongst the models (0.0-211.6 g C m⁻²; Fig. 1). For the R_{ANIMAL}, model differences tended to be smaller at lower input levels, especially when animal density was reduced without reductions in N fertilisation (0.0–143.9 g C m⁻²). For plant respiration (R_{PLANT}), an increase of model variability was associated with the reduced influence of the livestock. It is also interesting to note that net ecosystem exchange (NEE) values showed large variability among models with intermediate intensification levels, e.g. 70% reduction of LD and 40% reduction of N. The greatest variability was simulated under the mowing-dominated G5 site (Figs. A and B in supplementary material), but the model variability was also high under mowing and grazing combined management at G4 and under intensively grazed (by heifers) management at the G3 site. Reduction in N fertilization tended to decrease NEE variability at the G3 and G4 sites. In G5, the analysis of proportional changes indicated - with the combined reduction of N fertilisation and animal density - a clear linear decrease in NEE compared to the baseline (Fig. C in supplementary material). Since NEE is defined as the difference between ecosystem respiration (R_{ECO}) and gross primary production (GPP), the variability of its basic components have an effect on the spread of NEE values. The ensemble uncertainty of GPP and R_{ECO} were highest at G2, G3 and G4 sites, associated with the highest

animal densities (Table 2). This suggests that the intensification of grazing management tends to increase the variation of GPP and R_{ECO} estimates between models, with a smaller uncertainty envelope at the G1 and G5 sites, where altered animal density variation is very low ($0.1-0.04 \text{ LSU ha}^{-1} \text{ yr}^{-1}$).

The five grassland sites showed different dynamics in C fluxes with respect to the simulated management options, with NEE varying between -231.3 and $+189.2 \text{ g C m}^{-2} \text{ yr}^{-1}$, considering all sites and simulation years. These results suggest higher NEE ($-19.0 \pm 75.9 \text{ g}$ and $-47.6 \pm 89.8 \text{ g C m}^{-2} \text{ yr}^{-1}$ for baseline and LD_{50} , respectively), or lower C uptake, than Sousanna et al. (2007) concluded from nine European grassland sites equipped with eddy-covariance flux measurements, which showed an average net sink of atmospheric CO_2 with NEE of $-240 \pm 70 \text{ g C m}^{-2} \text{ yr}^{-1}$ (which is in the range -486.3 to $24.8 \text{ g C m}^{-2} \text{ yr}^{-1}$, or -1783 to $-91 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$, provided by Hörtnagl et al., 2018 for managed grasslands in Central Europe). The site-by-site analysis (Fig. C in supplementary material) indicated, except at the G5 site, that C uptake was the dominant process. At the G5 site, an NEE of <0 only occurred with $LD_{70}N_{40}$ management options. At this site, the greatest model uncertainty in NEE values occurred with the $LD_{70}N_{40}$ management option (Fig. 1), related to differently simulated CO_2 release and uptake processes. According to the median values, the G5 site reached the highest amount of C sequestration ($\sim 113.7 \text{ g C m}^{-2} \text{ yr}^{-1}$) at $LD_{50}N_0$. The general observation from the modelled sites of increasingly negative NEE in response to increasing N inputs is consistent with experimental observations that report increases in the flow of C to the soil in response to long-term fertiliser N use (Ammann et al. 2007; Skiba et al. 2013). For the period during which the C is sequestered, it is removed from the atmosphere and does not contribute to global warming. This effect is simulated at both grazed (G1, G2 and G3) and grazing dominated (G4) sites, for all scenarios. Owing to the large quantity of harvested aboveground biomass ($332.1 \pm 62.3 \text{ g DM m}^{-2} \text{ yr}^{-1}$ on average for the baseline scenario), the G5 site seems to

release C from the soil. However, the grazing removal ($395.8 \pm 38 \text{ g DM m}^{-2} \text{ yr}^{-1}$ on average for the baseline scenario of G3 site) may drive less radical changes in the C balance. Overall, these simulation results are consistent with eddy-covariance measurement data (Senapati et al., 2014; Koncz et al., 2017), in which mown treatments were observed to release C, whilst grazed treatments acted as net C sinks. For instance, in Senapati et al. (2014) mown treatments had lower annual net C storage ($22.7 \pm 32.3 \text{ g C m}^{-2} \text{ yr}^{-1}$, net sink), related to hay removal, than grazed plots ($140.9 \pm 69.9 \text{ g C m}^{-2} \text{ yr}^{-1}$, net sink) - though the observed site (Lusignan, France) was recently converted from cropland to grassland, so would be expected to be increasing in soil C (Senapati et al., 2014).

Considering all the sites, the estimated average C exchange (net biome productivity, NBP, Fig. 1) ranged between -176.9 (sink) and +140.4 $\text{g C m}^{-2} \text{ yr}^{-1}$ (source), with its extremes at LD₅₀N₀ and LD₆₀ management options, respectively. This high variability was caused by different management systems at G4 (grazed and mown) site (Figs. A and B in supplementary material), while the extensification combined with N reduction tended to increase C storage in some cases, e.g. at G5 site. Owing to the high organic C exports (from haycut and/or intensive cattle grazing: 1.34 and 1.21 LSU ha⁻¹ yr⁻¹), which could be greater than C imports from manure and slurry, the soil processes would be dominated by C emissions at the G2 site (intensive scenarios). The N mitigation reduced the net biome production at G3 site even further.

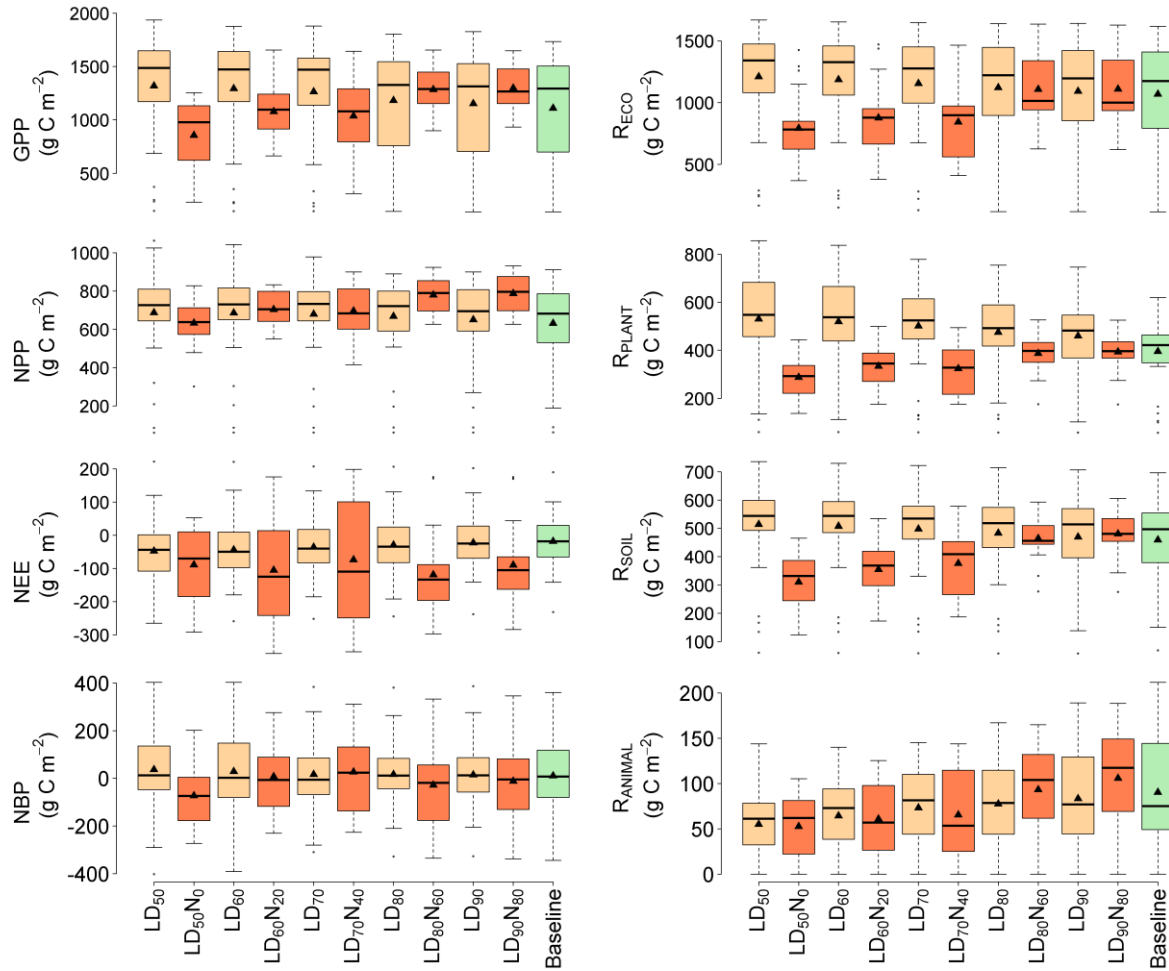


Fig. 1. Changes in CO₂ fluxes (g C m⁻²) calculated over multiple years at five sites, for ten altered management scenarios and the baseline (as in Table 3; LD: livestock density; N: nitrogen). For each management level, triangles show the multi-model (as in Table 4) mean, black lines show multi-model median. Boxes delimit the 25th and 75th percentiles. Whiskers are 10th and 90th percentiles. Points indicate outliers.

Ecosystem respiration (R_{ECO}), together with R_{PLANT} and R_{SOIL}, showed a linear decrease as LD and N levels simultaneously decreased, but tended to increase with a reduction in animal density only (Fig. 1). Animal respiration (R_{ANIMAL}) tended to decrease as animal density decreased, though the multi-model median line (Fig. 1) was associated with some uncertainty at the baseline and LD₇₀N₄₀ options (i.e. 30% less animals and 60% less N fertiliser). Site-by-site analyses showed (Figs. A and B in supplementary material) that the

greatest simulated R_{ECO} occurred with G3 and G4 grazing systems. Reduction in N fertilizer tended to decrease R_{ECO} , however the variability of soil respiration (R_{SOIL}) increased the uncertainty at G4, particularly under sheep-heifer grazing. Based on model simulations, the main losses of CO_2 at the G4 site were caused by R_{SOIL} and plant respiration (R_{PLANT}). Simulated yearly R_{ANIMAL} values, and their proportional changes (Fig. D in supplementary material) with respect to the baseline management showed a distinct emission decrease with extensification (which is not the case with R_{PLANT} and R_{SOIL} , Figs. A and B in supplementary material), at a quasilinear rate (by $y=-0.56+0.05x$, $R^2\sim 1$ for LD changes and $y=-0.62+0.05x$, $R^2=0.99$ for N and LD combined options at G3 site). The data also suggest that there were substantial differences among models in the estimated effects of altered management. These differences were amplified when N fertilization was decreased jointly with animal density (e.g. option $LD_{70}N_{40}$ at G4 and G5; Fig. D in supplementary material), which suggests that interactions between the two factors may make a sizeable contribution to this variability in the response of different models.

Some relationships between model outputs and management inputs were apparent from an analysis of data at each site. GPP decreased strongly with stocking rates while R_{ANIMAL} increased, with the exception of G2 site (Fig. E in supplementary material). The simulated outputs at this site may reflect different and non-linear responses of alternative models (Fig. F in supplementary material). Often, the offtake increased and NPP decreased with management intensification, albeit with large differences between models. With M06, the highest Offtake was simulated when animal density decreased by 30%, while this happened at 10% lower animal density with M24. M08 simulated the highest NPP value at 30% less livestock density, while with M28 the highest NPP values were simulated at the most intensive management condition.

The influence of N fertilization was investigated at G3, G4 and G5 sites (Fig. 2) by comparing the combined effect of livestock density reduction and N fertilisation reduction. In terms of GPP (Fig. 2) and NPP (Fig. L in supplementary material), the simulations showed a considerable decrease in GPP with >60% less applied N fertilizer at site G4. The R_{ECO} (Fig. 3, middle panel) values also decreased with extensification, where the N reduction had a greater effect at the G3 and G4 sites. Animal respiration was driven by livestock density (Fig. G in supplementary material), while soil and plant respiration were mainly influenced by N inputs (lower R_{PLANT} and R_{SOIL} with lower N inputs). In terms of NEE (Fig. 2, lower panel) and NBP (Fig. G in supplementary material) the trend was less obvious, owing to differences in management and site conditions.

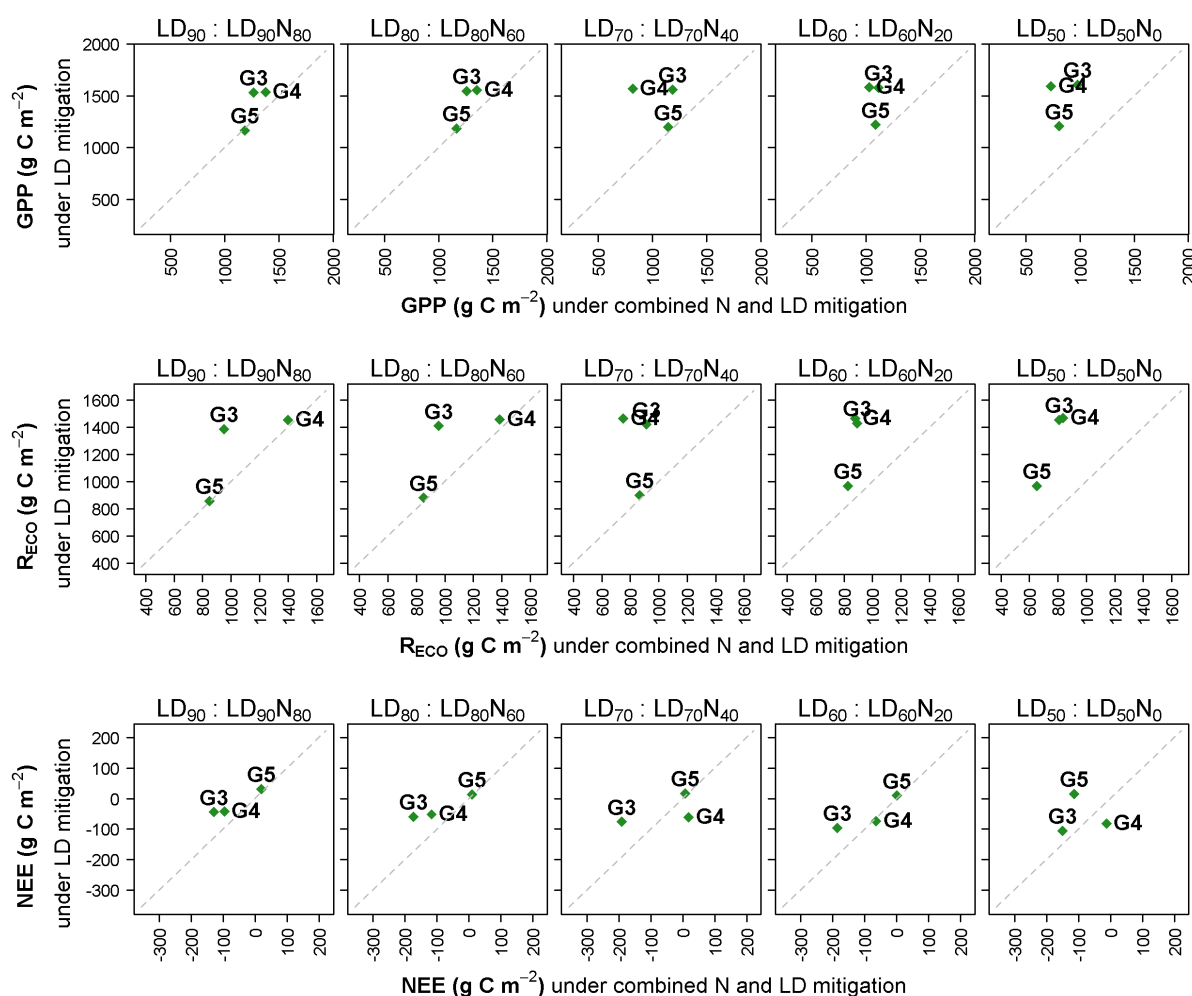


Fig. 2. Comparison of the combined effect of livestock density reduction (LD from 90% down to 50% of initial density) and the N fertilisation reduction (N from 80% down to 0% of initial amount) at G3, G4 and G5 sites for gross primary production (GPP), ecosystem respiration (R_{ECO}) and net ecosystem exchange (NEE) using the multi-model median.

The effectiveness of the different management strategies such as fertilizer amounts, different animal stocking rates, grazing alone or combined with mowing, was also influenced by site-specific soil (type and depth) and weather conditions (ie. Precipitation). If we are to distinguish between environmental from management effects, then precipitation patterns must be taken into account as it can also have an influence on the results of the CO_2 fluxes (e.g. Polley et al., 2010). In our simulation study, the amount of precipitation showed a positive correlation with R_{SOIL} and all the other investigated CO_2 fluxes (Fig. H in supplementary material) apart from NEE and NBP. The respiration outputs demonstrated higher sensitivity to N fertilization, than to percent livestock density changes. NEE values suggested greater respiration in very arid years (such as some years at G1 site, where annual mean precipitation was 271 ± 141 mm), where the animal density reduction did not reduce the amount of CO_2 emissions. A recent review highlighted the particular sensitivity of warm and dry climates to change in stocking density where increased livestock density was associated with significantly lower rates of C sequestration (Abdalla et al., 2018). Gilmanov et al. (2007) pointed out that organic and semi-arid grassland sites have the potential to become C sources. With decreasing stocking rate, NEE tended to increase above 800 mm annual precipitation. In humid and very humid years, the soil may be saturated and anaerobic, and organic C decomposition can be slowed or stopped under these conditions (yet anaerobic decomposition of partly decomposed organic matter may emit methane, e.g. Bannert et al., 2012). The variability of NEE decreased

with N reduction, e.g. the most extensive treatment showed the smallest difference from zero (Fig. H in supplementary material).

3.2. *Non-CO₂ fluxes*

A recent IPCC report (2014) and other analyses (Schulze et al., 2009; Tubiello et al., 2014; Gerber et al., 2015; Hörtnagl et al., 2018) highlight the importance of the reduction of non-CO₂ GHGs, as an important element of agricultural mitigation strategies. Particularly methane and nitrous oxide cause longer-term warming effects than CO₂. There were clear trends in model responses, indicating decreases in N₂O-N, NH₃-N, NO_x-N, N₂ and NO₃-N leaching with reductions in N fertilizer, while there were no clear trends in the response to animal livestock reduction (Fig. 3, all models and sites confounded). Only NO₃-N leaching showed a distinctly linear decrease with simultaneous decreases of N fertiliser and livestock density, suggesting a close dependance of this output on N fertilization input. Methane (CH₄-C) emissions tended to decrease with decreasing livestock density and also with reductions in N fertilisation.

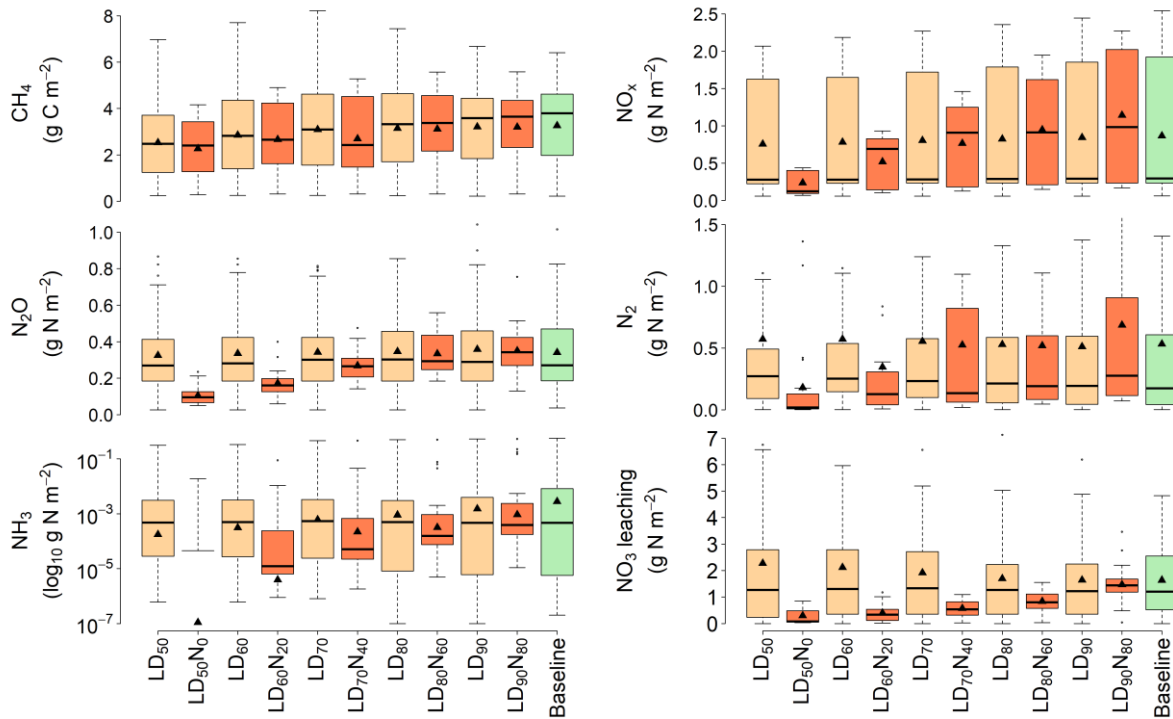


Fig. 3. Changes in non-CO₂ fluxes (g C m⁻², g N m⁻², log₁₀ g N m⁻²) calculated over multiple years at five sites, for ten altered management scenarios and the baseline (as in Table 3). For each management level, triangles show the multi-model (as in Table 4) mean, black lines show multi-model median. Boxes delimit the 25th and 75th percentiles. Whiskers are 10th and 90th percentiles. Hollow circles indicate outliers (LD from 90% down to 50% of initial density, N fertilisation from 80% to 0% of initial amount).

For N₂O emissions, relative effect size analysis (Fig. I in supplementary material) and simulated emissions (Fig. 4 and Fig. J in supplementary material, respectively) revealed linear decreasing trends as both livestock density and N fertiliser were reduced (sites G3, G4 and G5, Fig. 4, bottom). The greatest mitigation of N₂O-N emission was obtained by reductions in N fertilizer at the G4 and G5 sites, where the initial 0.51 and 0.63 g N₂O-N m⁻² were reduced to 0.11 and 0.16 g N₂O-N m⁻², respectively. In terms of total GHG emissions, using the 100-year Global Warming Potential (GWP₁₀₀), the N mitigation from baseline to zero would reduce the multi-model median simulated N₂O emissions by 135.7, 187.1 and 219.9 g CO₂e

m⁻² yr⁻¹ at G3, G4 and G5 sites, respectively. This corresponds to ~16–25% of C sink potential, reported by Soussana et al. (2007) across nine European grassland sites, but a larger percentage (~40–65%) of the sink potentials determined in this study.

The reduction of N fertilizer logically decreases the N₂O-N emissions, as reported here (Fig. J in supplementary material) and by experimental studies (Cardenas et al., 2010; Bell et al., 2016; Hörtnagl et al., 2018). Our results at the G3 site showed the same trend (Table 5), when the N₂O-N emissions are compared to the applied N fertilizer amounts, the estimated (simplified) N₂O-N emission factors (percent ratios of the total yearly N₂O-N emissions over the amount of annually applied N fertiliser, both in kg N ha⁻¹). Our simulated results (varying between 1.0 and 3.5% across sites and treatments) are not far from the IPCC (2006) default EF for fertilizer N value, which is 1%. At G4 and G5 sites, the EF values tended to increase as grassland management received less N fertilizer (Table 5), which suggest some non-linear reduction of N₂O under reduced fertiliser supply, which can be explained by a decrease of plant N uptake with decreasing N fertilizer rate (e.g. Lü et al., 2014). Negative relationships between N use efficiency and soil N availability were observed in a variety of ecosystems, including grasslands (e.g. Yuan et al., 2006). Decreased N uptake from the soil and less efficient use of the N assimilated by plants leave more N available for microbes in the soil (which is the most important factor for N₂O-N emissions). Thus, the most intensive systems (G3, G4 and G5) had the highest CO₂e emission rates while the N₂O-N emission factors varied between the managements options. There was no trend in median values of simulated N₂O emissions and LD levels, with the exception of G1 and G4 (Fig. I in supplementary material). At the G1 site, a slight decreasing trend was noticeable with decreasing grazing intensity, with increasingly diverging results among models as more extensive management was introduced.

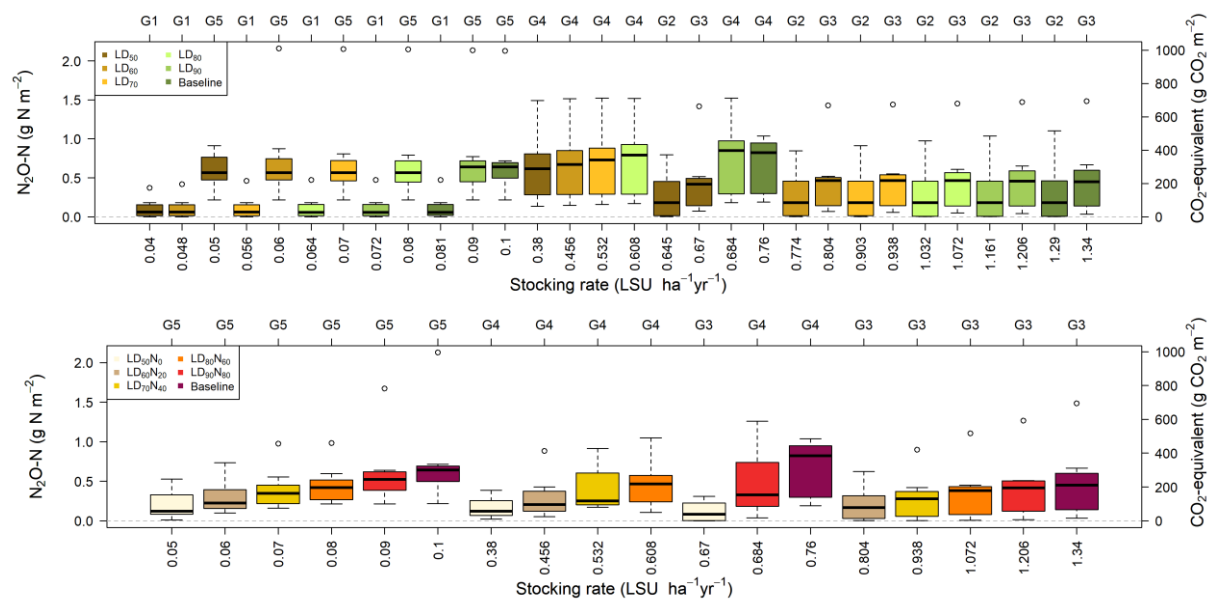


Fig. 4. Relationship between nitrous oxide emissions (multi-year averages of seven models) given in N_2O-N and CO_2e forms, and increasing animal stocking rate at all sites comparing livestock density reductions (top graph) and livestock density and N fertilization reduction (bottom graph), as in Table 3.

Table 5. N_2O-N emission factors: multi-model median at the three N fertilised sites (as in Table 2). Grey cells indicate the lowest values.

Management options	G3	G4	G5
Baseline	1.3%	1.8%	2.3%
LD ₉₀ N ₈₀	1.4%	1.2%	2.0%
LD ₈₀ N ₆₀	1.6%	2.0%	1.9%
LD ₇₀ N ₄₀	1.4%	2.2%	2.5%
LD ₆₀ N ₂₀	1.0%	1.7%	3.5%
LD ₅₀ N ₀	-	-	-

Overall, the different N fluxes (Fig. 4 and Fig. K in supplementary material) tended to decrease with reduced N fertilization, mainly after a 60% reduction in the amount of N applied in both grazed and combined (mown and grazing) systems.

Regarding CH_4-C emissions (Fig. 5), the G3 site had much higher model uncertainty than other sites, mostly due to high estimates from M06 and M24. The simulated multi-model

425 median values were the highest, with lower livestock density. For example, the multi model
426 multi-year average baseline simulation was 4.6 g C m^{-2} , which was reduced to 3.6 g C m^{-2}
427 with stocking rate reduction alone, and to 3.4 g C m^{-2} in combination with N reduction at the
428 G3 site (Fig. 5). The main agricultural source of CH_4 at the G3 site was the intensive heifer
429 grazing system. Other sites were less affected because either they had grazing sheep (G2 and
430 G5) or were less intensively grazed (low cattle density in G1, combined sheep and cattle
431 grazing in G4).

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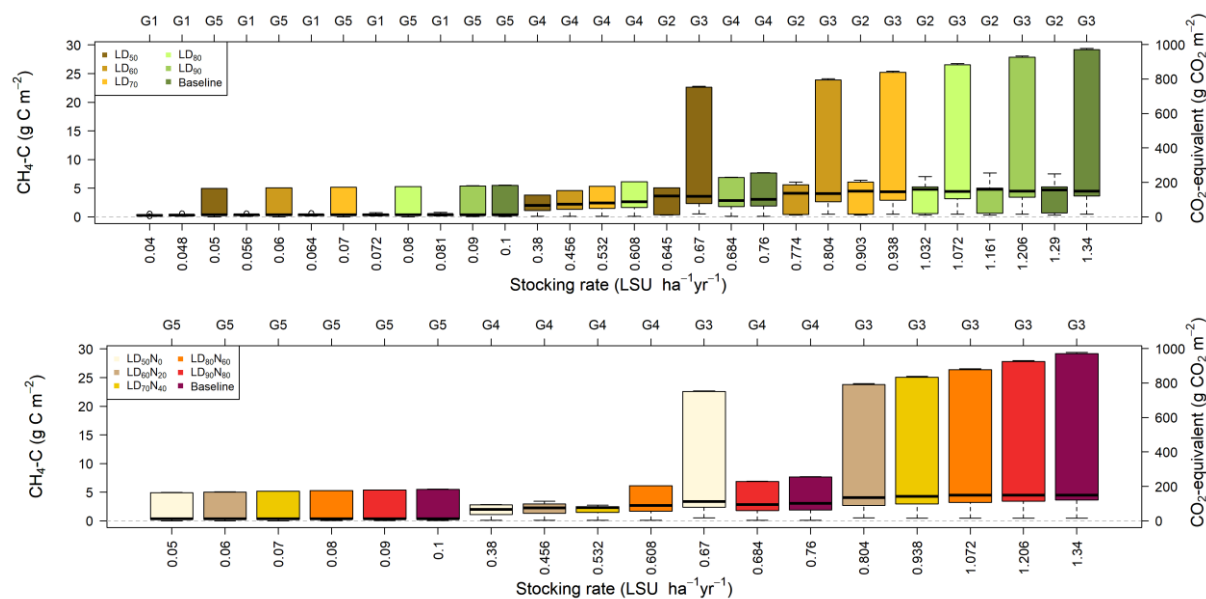


Fig. 5. Relationship between methane emissions (multi-year averages of five models), expressed as CH₄-C and CO₂e, and increasing animal stocking rate at all sites, comparing livestock density reduction (top graph) and livestock and N fertilization reduction (bottom graph) as given in Table 3.

Site-specific circumstances, mainly soil properties (particularly soil N availability), and precipitation patterns, have considerable effect on the N balance of the grassland sites. Our modelled outputs show that soils tended to release more N₂O-N and CH₄-C (Fig. L in supplementary material) in humid and very humid years, while the net N emissions were lower during drier years. The highest N₂O-N emissions and also N₂ and NO_x emissions (Fig. L in supplementary material) were simulated when annual precipitation was around 1000 mm, owing to the more available N, because high rainfall rates increase the rate of N transport to deeper soil layers and increase nitrate leaching (Fig. L in supplementary material). Also, there would be more anaerobic microsites leading to greater rates of denitrification in waterlogged soils (Smith et al., 1998). Besides, higher NPP values (Fig. H in supplementary material) were associated with elevated precipitation, thus higher organic N inputs to soil may contribute to the larger N₂O-N emissions. This indicates that the intensity of N losses tends to be associated

with annual precipitation levels, and N losses can be effectively mitigated by reducing livestock density and/or N fertilisation rates. Our simulations indicate reductions in N fertilization as the most effective option for mitigating non-CO₂ fluxes, mainly in humid areas, an observation that is consistent with a number of previous studies (Bouwman et al., 2002; Rees et al., 2013) but further studies are required considering the high variability of model responses.

3.3. Productivity and energy outputs

Some decreasing trends with management extensification can be observed in the box-plots of Fig. 6, e.g. for simulated Offtake and Intake, whilst aboveground and belowground biomass increased with lower stocking rates, combining simulation results from five sites. In terms of harvested aboveground biomass, a drop was simulated with no N fertilization (e.g. baseline simulation: 421.7±118.6 g DM m⁻², LD₅₀N₀ management: 200.9±78.8 g DM m⁻² across the multi-year site averages).

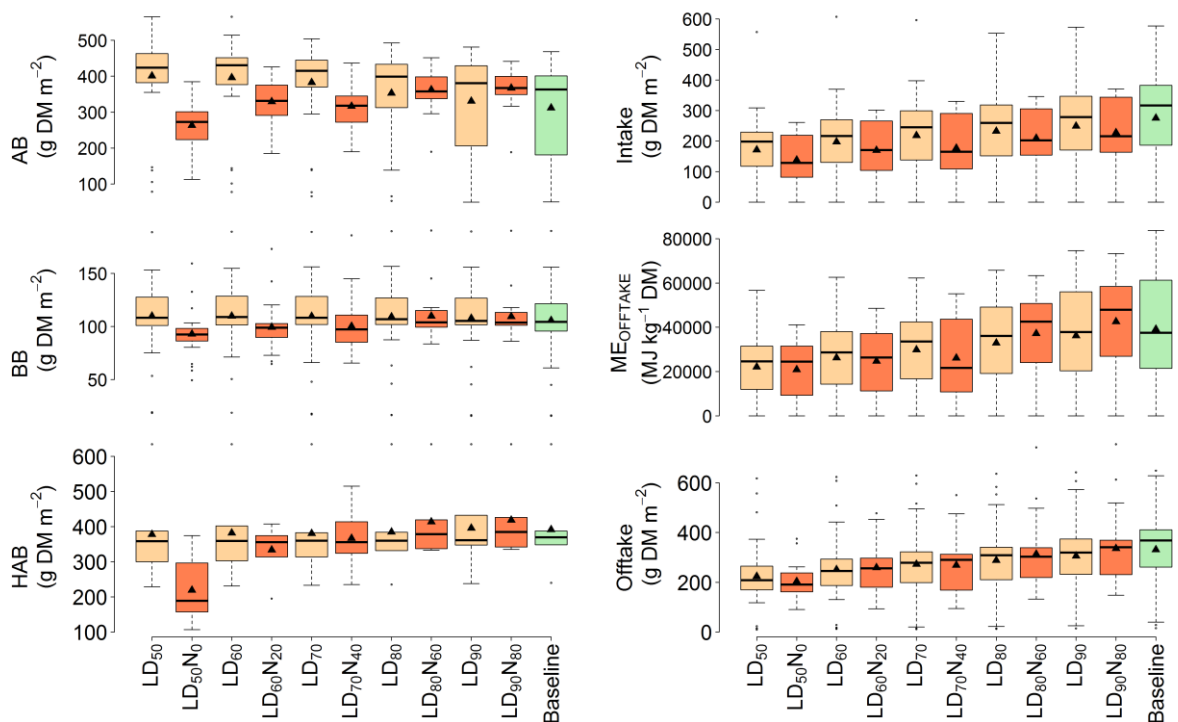


Fig. 6. Changes in productivity and energy outputs (g DM m^{-2} , $\text{MJ kg}^{-1} \text{ DM}$) calculated over multiple years at five sites, for ten altered management scenarios and the baseline (as in Table 3). For each management level, triangles show the multi-model (as in Table 4) mean, black lines show multi-model median. Boxes delimit the 25th and 75th percentiles. Whiskers are 10th and 90th percentiles. Points indicate outliers.

In fertilised sites, where LD levels have been assessed alone and in combination with N fertilisation levels, Fig. 6 and Fig. M in the supplementary material indicate that, overall, reducing N fertiliser rate will have more effect on aboveground biomass and biomass offtake than reducing livestock density, as data points relative to sites G3, G4 and G5 tend to stay below the 1:1 line. The effect of N fertiliser reduction starts becoming visible at G4 with 60% N reduction, while only with no N fertilisation is this effect visible at G5. However, livestock density reduction has a greater effect on animal intake, belowground biomass and $\text{ME}_{\text{Offtake}}$ (Fig. M in supplementary material). Animal intake decreases considerably with extensification (Fig. 6 and Fig. N in supplementary material).

The annual NPP values, normalized by animal stocking rates, are shown in Fig. 7 for each management option (Fig. 7). The G5 site (mowing dominated) was excluded from this analysis owing to the very low stocking rate practised at this site, thus a relationship was established of animal intake (not offtake) with NPP over stocking rate ratio. There was a decreasing trend in animal intake with extensification when animals have access to more biomass per head. This trend is also supported by the relationship between the minimum required amount of biomass per animal and the productivity of the sites under different management options. Using $1.5 \text{ LSU ha}^{-1} \text{ yr}^{-1}$ as an overall reference estimate of potential ecological carrying capacity (e.g. UK Rural Payments Agency, 2003), which is equal to 1.5 adult cattle on 1 ha pasture field, we see that around ~46% of the total biomass produced each

year is consumed by animals in the most intensive grazing systems (baseline) of G2 and G3 sites (Figure 7). With extensification, this ratio is reduced to ~23% at LD₅₀ (average of G2 and G3 sites).

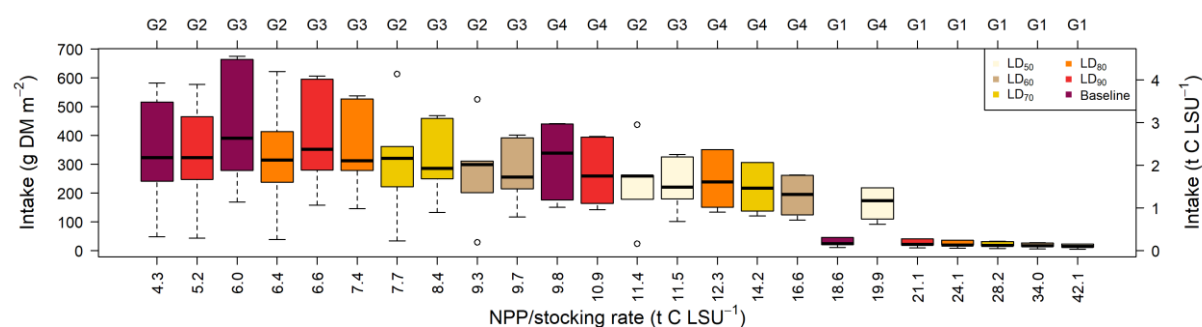


Fig. 7. Relationship between animal intake (Intake) (multi-year averages of eight models, expressed with two units) and the ratio of net primary production (NPP) (multi-year averages of eight models) over animal stocking rate for different livestock densities (as in Table 3).

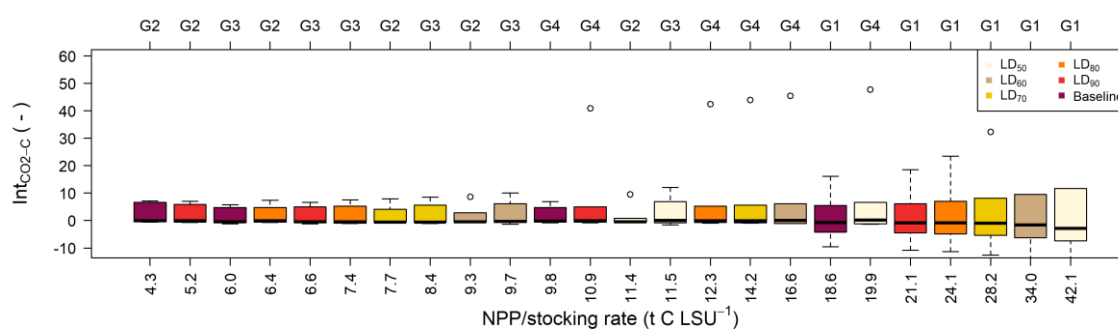
Overall, grassland productivity increases with annual precipitation levels, though uncertainties can be large (e.g. seasonal waterlogging spells and heat waves may have negative effects on grassland productivity also with rainfall >1000 mm yr⁻¹), indicating higher sensitivity to animal density reduction (which has some positive effects) than to N fertilization reduction (with even greater negative effects) of ME_{Offtake}, Intake, Offtake, AB and BB (Fig. O in supplementary material).

3.4. CO₂, CH₄ and N₂O intensities

Extensification, mostly through N input reduction, increased the variability of results in the case of methane intensity. Overall, N₂O-N intensity reduces with greater extensification (Fig. P in supplementary material), mainly driven by N fertilizer reduction, while CO₂-C intensity shows different patterns at each site. In G4, in particular, CO₂-C intensity is >1 when

animal density was reduced by 60%. Multi-model median simulations suggest that reducing N fertilization does not affect methane emissions. However, at the G3 site (grazed by heifers), which shows the greatest intensities (Fig. Q in supplementary material), CH₄-C emissions increase with reducing animal density (with cattle having a larger area to graze, and thus more biomass available for feeding).

For N₂O-N intensity (Fig. R in supplementary material), model variability increased with reductions in animal density at the G1 and G3 sites (cattle grazing systems). Under sheep grazing (G2, G4, G5 sites), different models did not differ much in their output when reducing animal density. The intensity of C (in the form of CO₂-C and CH₄-C) and N (in the form of N₂O-N) emissions with respect to biomass offtake did not change with extensification (Fig. P in supplementary material). The plot of CH₄-C intensity values against NPP-stocking rate ratios (Fig. 8) show the extensification at G3 site increased the simulation uncertainty. For sheep grazing systems, methane emissions did not vary greatly with management options. However, CO₂-C and N₂O-N intensities, and their simulation uncertainties, increased with extensification, when animals had more available biomass.



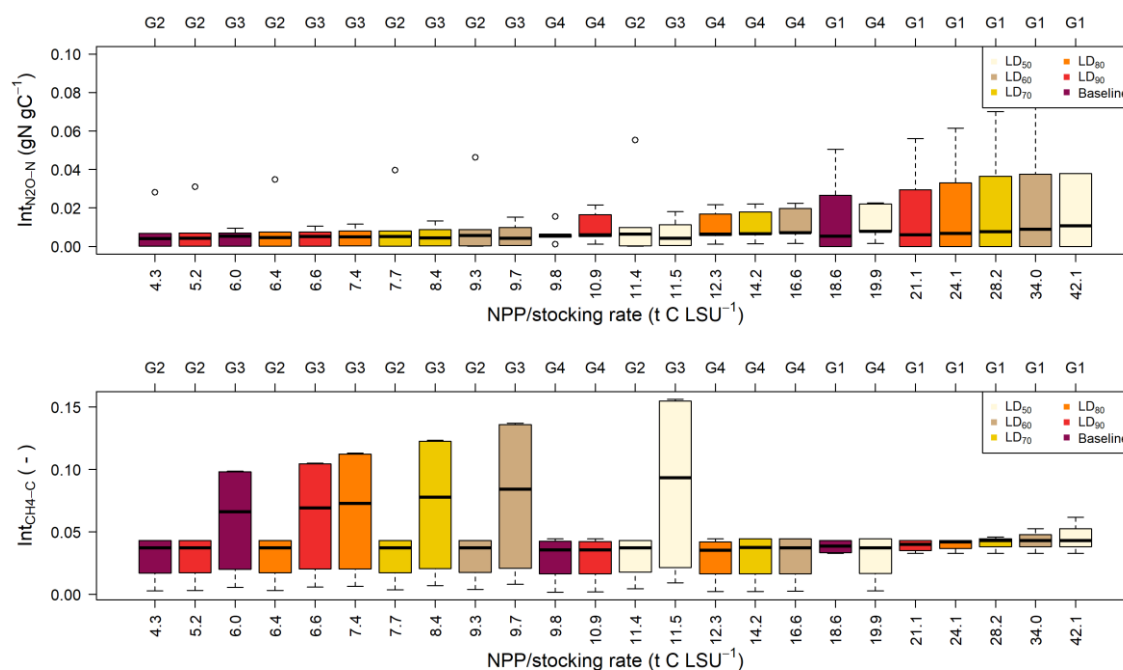


Fig. 8. Relationship between CO₂-C, N₂O-N and CH₄-C intensity outputs (multi-year averages of eight, seven and five models, respectively) and the ratio of net primary production (NPP) output and animal stocking rate for different livestock densities (as in Table 3).

In relation to annual precipitation levels, CO₂-C, CH₄-C and N₂O-N intensities (Fig. R in supplementary material) showed different patterns for arid and humid conditions. In the case of CO₂-C intensity, C sequestration was moving around its equilibrium at humid conditions, whilst for drier years it showed different patterns. N fertilization reduction may increase C fixation, with its maximum at 30% less animal density and 60% less N fertilization.

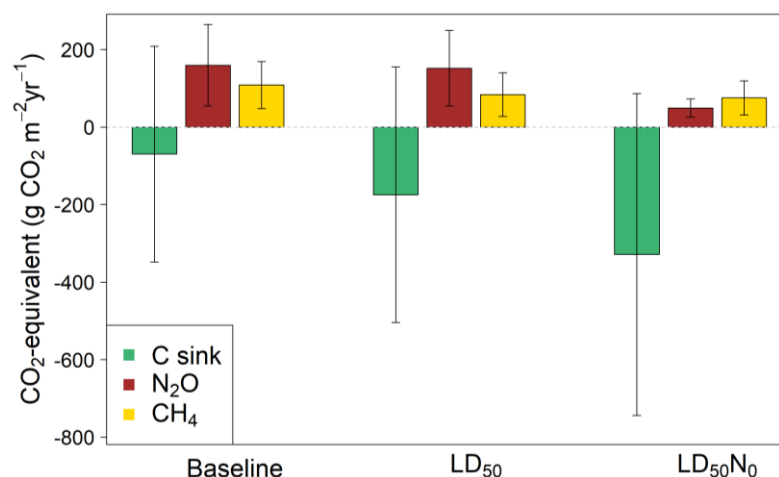


Fig. 9. Ensemble modelling of carbon sink (C sink), nitrous oxide emissions (N₂O) and methane emissions (CH₄) in CO₂eq form using multi-site averages of the multi-model median of eight models under grassland mitigation options (as in Table 3).

Overall, the carbon sink increased with extensification (baseline: ~-70, LD₅₀: ~-175 and LD₅₀N₀: ~-329 CO₂eq) (Fig.9), but N₂O and CH₄ emissions decreased. Livestock density reduction showed greater effect on CH₄-CO₂eq reduction (baseline: ~108, LD₅₀: ~84 and LD₅₀N₀: ~75 CO₂eq), while N fertilization reduction considerably reduced the N₂O emission from ~160 and ~152 CO₂eq (baseline and LD₅₀, respectively) to ~49 CO₂eq with no N fertilisation.

4. Summary and conclusions

This is the first multi-model study to simulate the effect on C and N fluxes of reduced grazing intensity and N fertiliser inputs in multiple grassland systems across the globe. By mobilizing a multi-model approach, it has provided an improved understanding of GHG flux dynamics in pastures. This study confirms that grasslands (which have the advantage of potentially acting as a C and N sink compared to many croplands) can be exploited for GHG

mitigation in beef and dairy production, because C and N sequestrations can, under some circumstances, offset GHG emissions.

Simulated C fluxes indicated that there may be some shift towards a C sink ($NEE < 0$) with decreasing inputs, though it depends on complex, multifaceted processes of C fixation (GPP) and release (R_{ECO}) occurring in the ecosystem. This is especially true for G3 and G4 sites, while grasslands managed with low animal densities may not support C sequestration under arid conditions or in the presence of high organic C exports from mowing. Simulated N outputs showed the considerable effect of N fertilizer reduction on C and N emissions, while changes in animal density only slightly affected the N balance. Both simulated CH_4 -C and N emissions (including leaching) were, as expected, highly sensitive to precipitation levels, with higher values being seen under humid conditions (annual precipitation > 1000 mm). This indicates the importance of considering climate patterns when determining budgets of C and N under varying management options. With the most intensively grazed systems, ~35-40% of the simulated net primary production was grazed by animals, with this ratio decreasing to ~13% with decreasing stocking rates. The greatest enteric CH_4 -C intensities were estimated for intensive grazing systems, whilst the highest estimates of N_2O -N intensities were found for mown and extensively grazed arid systems. Considering the dynamic behaviour of grassland systems, the amounts of C and N sequestered or released are not the same each year. However, uncertainties in the year-to-year variations are not critical in this context as our focus was on capturing major trends and levels rather than modelling exact annual or seasonal fluxes.

While suggesting the possibility of using models to determine sound mitigation practices, the present study also showed limitations. Our findings are based purely on simulated data and lack evaluation against measured outputs (experimental trials that have appeared in the published literature give us, at a minimum, a hint at what comprehensive

assessment of multi-model ensemble would look like). Although the models used in this study are only a subset of the available grassland models, we think that the various model types and variants (and related parameterizations) evaluated here are reasonably representative of current approaches. Another study limitation is that grassland practices other than grazing density and N fertilisation were not assessed. For instance, an option that has not been accounted for in this study is increasing the proportion of legume species in the sward which can allow for reduced use of N fertiliser, and has the potential to mitigate GHG emissions (e.g. Lanigan et al., 2013; Fuchs et al., 2018). For an analysis of the mitigation potential of legumes, we refer readers to a parallel study underway as part of the Model4Pastures project (<https://www.faccejpi.com/Research-Themes-and-Achievements/GHG-Mitigation/multi-partners-call/Models4Pastures>). Other options, such as organic N fertilisation, nitrification inhibitors or supplemental feeding, which are common practices in grassland management, have been left out given that state-of-the-art models are not unambiguously sensitive to such management interventions (Brilli et al., 2017). These difficulties, and those associated with model-to-model variability, suggest that some development work would be sensible given the importance of grasslands in supporting the broader GHG emissions reduction agenda. Despite their limitations, biogeochemical models (which evolve with the progress of research) are today a valuable tool for evaluating alternative options for mitigation of GHG emissions through grassland management. It is still rare for results in support to management decisions to be reported by an assessment of uncertainty. Our results show the potential for associating quantification of uncertainties with the results of grassland modelling under alternative management.

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References

Abdalla, M., Hastings, A., Chadwick, D.R., Jones, D.L., Evans, C.D., Jones, M.B., Rees,
 R.M., Smith, P., 2018. Critical review of the impacts of grazing intensity on soil organic
 carbon storage and other soil quality indicators in extensively managed grasslands.
 Agriculture, Ecosystems and Environment 253, 62-81.

Abdalla, M., Richards, M., Pogson, M., Smith, J.U., Smith, P., 2017. Estimating the effect of
 nitrogen fertilizer on the greenhouse gas balance of soils in Wales under current and future
 climate. Regional Environmental Change 16, 2357-2368.

Allard, V., Soussana, J.-F., Falcimagne, R., Berbigier, P., Bonnefond, J.M., Ceschia, E.,
 D'hour, P., Hénault, C., Laville, P., Martin, C., Pinarès-Patino, C., 2007. The role of
 grazing management for the net biome productivity and greenhouse gas budget (CO₂, N₂O
 and CH₄) of semi-natural grassland. Agriculture, Ecosystems and Environment 12, 47-58.

Ammann, C., Flechard, C.R., Leifeld, J., Neftel, A., Fuhrer, J., 2007. The carbon budget of
 newly established temperate grassland depends on management intensity. Agriculture,
 Ecosystems and Environment 121, 5-20.

Atkinson, P.W., Fuller, R.J., Vickery, J.A., Conway, G.J., Tallowin, J.R.B., Smith, R.E.N.,
 Haysom, K.A., Ings, T.C., Asteraki, E.J., Brown, V.K., 2005. Influence of agricultural
 management, sward structure and food resources on grassland field use by birds in lowland
 England. Journal of Applied Ecology 42, 932-942.

Bell, M.J., Cloy, J.M., Topp, C.F.E., Ball, B.C., Bagnall, A., Rees, R.M., Chadwick, D.R.,
 2016. Quantifying N₂O emissions from intensive grassland production: the role of
 synthetic fertiliser type, application rate, timing, and nitrification inhibitors. Journal of
 Agricultural Science 154, 812-827.

Ben Touhami, H., Bellocchi, G., 2015. Bayesian calibration of the Pasture Simulation model
 (PaSim) to simulate European grasslands under water stress. Ecological Informatics 30,
 356-364.

659 Bannert, A., Bogen, C., Esperschuetz, J., 2012. Anaerobic oxidation of methane in grassland
660 soils used for cattle husbandry. *Biogeosciences* 9, 3891-3899.

661 Bondeau, A., Kicklighter, D.W., Kaduk, J. and the participants of the Potsdam NdP Model
662 Intercomparison, 1999. Comparing global models of terrestrial net primary productivity
663 (NPP): importance of vegetation structure on seasonal NPP estimates. *Global Change*
664 *Biology* 5, 35-45.

665 Bondeau, A., Smith, P.C., Zaehle, S., Schaphoff, S., Lucht, W., Cramer, W., Gerten, D.,
666 Lotze-campen, H., Müller, C., Reichstein, M., Smith, B., 2007. Modelling the role of
667 agriculture for the 20th century global terrestrial carbon balance. *Global Change Biology*
668 13, 679-706.

669 Bouwman, A.F., Boumans, L.J.M., Batjes, N.H., 2002. Emissions of N₂O and NO from
670 fertilized fields: Summary of available measurement data. *Global Biogeochemical Cycles*
671 16, art-1058.

672 Brilli, L., Bechini, L., Bindi, M., Carozzi, M., Cavalli, D., Conant, R., Dorich, C.D., Doro, L.,
673 Ehrhardt, F., Farina, R., Ferrise, R., Fitton, N., Francaviglia, R., Grace, P., Iocola, I.,
674 Klumpp, K., Léonard, J., Martin, R., Massad, R.S., Recous, S., Seddaiu, G., Sharp, J.,
675 Smith, P., Smith, W.,N., Soussana, J.-F., Bellocchi, G., 2017. Review and analysis of
676 strengths and weaknesses of agro-ecosystem models for simulating C and N fluxes.
677 *Science of the Total Environment* 598, 445-470.

678 Calanca, P., Vuichard, N., Campbell, C., Viovy, N., Cozic, A., Fuhrer, J., Soussana, J.-F.,
679 2007. Simulating the fluxes of CO₂ and N₂O in European grasslands with the Pasture
680 Simulation Model (PaSim). *Agriculture, Ecosystems and Environment* 121, 164-174.

681 Calanca, P., Deléglise, C., Martin, R., Carrère, P., Mosimann, E., 2016. Testing the ability of
682 a simple grassland model to simulate the seasonal effects of drought on herbage growth.
683 *Field Crops Research* 187, 12-23.

684 Campbell, E.E., Paustian, K., 2015. Current developments in soil organic matter modeling
685 and the expansion of model applications: a review. *Environmental Research Letters* 10,
686 123004.

687 Cardenas, L.M., Thorman, R., Ashlee, N., Butler, M., Chadwick, D., Chambers, B., Cuttle, S.,
688 Donovan, N., Kingston, H., Lane, S., Dhanoa, M.S., Scholefield, D., 2010. Quantifying
689 annual N₂O emission fluxes from grazed grassland under a range of inorganic fertiliser
690 nitrogen inputs. *Agriculture, Ecosystems and Environment* 136, 218-226.

691 Challinor, A.J, Smith, M.S., Thornton, P., 2013. Use of agro-climate ensembles for
692 quantifying uncertainty and informing adaptation. *Agricultural and Forest Meteorology*
693 170, 2-7.

694 Chang, J., Ciais, P., Viovy, N., Vuichard, N., Herrero, M., Havlik, P., Wang, X., Sultan, B.,
695 Soussana, J.-F. (2015) Effect of climate change, CO₂ trends, nitrogen addition, and land-
696 cover and management intensity changes on the carbon balance of European grasslands.
697 *Global Change Biology* 22, 338-350.

698 Chang, J., Viovy, N., Vuichard, N., Ciais, P., Wang, T., Cozic, A., Lardy, R., Graux, A.-I.,
699 Klumpp, K., Martin, R., Soussana, J.-F., 2013. Incorporating grassland management in
700 ORCHIDEE: model description and evaluation at eddy-covariance sites in Europe.
701 *Geoscientific Model Development* 6, 2165-2181.

702 Chen, D.L., Li, Y., Grace, P., Mosier, A.R., 2008. N₂O emissions from agricultural lands: a
703 synthesis of simulation approaches. *Plant and Soil* 309, 169-189.

704 Churkina, G., Running, S.W., Schloss, A.L. and the participants of the Potsdam NdP Model
705 Intercomparison, 1999. Comparing global models of terrestrial net primary productivity
706 (NPP): the importance of water availability. *Global Change Biology* 5, 46-55.

707 Ciais, P., Soussana, J.-F., Vuichard, N., Luyssaert, S., Don, A., Janssens, I.A., Piao, S.L.,
708 Dechow, R., Lathière, J., Maignan, F., Wattenbach, M., Smith, P., Ammann, C., Freibauer,

709 A., Schulze, E.D. and the CARBOEUROPE Synthesis Team, 2010. The greenhouse gas
 710 balance of European grasslands. *Biogeosciences Discussions* 7, 5997-6050.

711 Clark, H, Brookes, I, Walcroft, A., 2003. Enteric methane emissions from New Zealand
 712 ruminants 1990–2001 calculated using an IPCC Tier 2 approach. Report prepared for the
 713 Ministry of Agriculture and Forestry by AgResearch and Massey University, Ministry of
 714 Agriculture and Forestry, Wellington, New Zealand.

715 Elliott, J., Müller, C., Deryng, D., Chryssanthacopoulos, J., Boote, K.J., Büchner, M., Foster,
 716 I., Glotter, M., Heinke, J., Iizumi, T., Izaurralde, R.C., Mueller, N.D., Ray, D.K.,
 717 Rosenzweig, C., Ruane, A.C., Sheffield, J., 2015. The Global Gridded Crop Model
 718 Intercomparison: data and modeling protocols for Phase 1 (v1.0). *Geoscientific Model*
 719 *Development* 8, 261-277.

720 Ehrhardt, F., Soussana, J.-F., Bellocchi, G., Grace, P., Mcauliffe, R., Recous, S., Sandor, R.,
 721 Smith, P., Snow, V., Migliorati, M.D., Basso, B., Bhatia, A., Brill, L., Doltra, J., Dorich,
 722 C.D., Doro, L., Fitton, N., Giacomini, S.J., Grant, B., Harrison, M.T., Jones, S.K.,
 723 Kirschbaum, M.U., Klumpp, K., Laville, P., Leonard, J., Liebig, M.A., Lieffering, M.,
 724 Martin, R., Massad, R., Meier, E., Merbold, L., Moore, A.D., Myrghiotis, V., Newton, P.,
 725 Pattey, E., Rolinski, S., Sharp, J., Smith, W.N., Wu, L., Zhang, Q., 2018. Assessing
 726 uncertainties in crop and pasture ensemble model simulations of productivity and N₂O
 727 emissions. *Global Change Biology* 24, e603-e616.

728 FAO, 2014. World reference base for soil resources 2014. *World Soil Resources Report* 106
 729 Rome. 120 pp.

730 Folberth, C., Skalský, R., Moltchanova, E., Balkovič, J., Azevedo, L.B., Obersteiner, M., van
 731 der Velde, M., 2016. Uncertainty in soil data can outweigh climate impact signals in global
 732 crop yield simulations. *Nature Communications* 7, 11872.

- Fuchs, K., Hörtnagl, L., Buchmann, N., Eugster, W., Snow, V., Merbold, L., 2018. Management matters: Testing a mitigation strategy for nitrous oxide emissions on intensively managed grassland. *Biogeosciences Discussions*, <https://doi.org/10.5194/bg-2018-192>.
- Gerber, P.J., Mottet, A., Opio, C.I., Falcucci, A., Teillard, F., 2015. Environmental impacts of beef production: Review of challenges and perspectives for durability. *Meat Science* 109, 2-12.
- Giardina, C.P., Litton, C.M., Crow, S.E., Asner, G.P., 2014. Warming-related increases in soil CO₂ efflux are explained by increased below-ground carbon flux. *Nature Climate Change* 4, 822-827.
- Gilmanov, T., Soussana, J.-F., Aires, L., Allard, V., Ammann, C., Balzarolo, M., Barcza, Z., Bemhofer, C., Campbell, C.L., Cernusca, A., Cescatti, A., Clifton-Brown, J., Dirks, B.O.M., Dore, S., Eugster, W., Fuhrer, J., Gimeno, C., Gruenwald, T., Haszpra, L., Hensen, A., Ibrom, A., Jacobs, A.F.G., Jones, M.B., Lanigan, G., Laurila, T., Lohila, A., Manca, G., Marcolla, B., Nagy, Z., Pilegaard, K., Pinter, K., Pio, C., Raschi, A., Rogiers, N., Sanz, M.J., Stefani, P., Sutton, M., Tuba, Z., Valentini, R., Williams, M.L., Wohlfahrt, G., 2007. Partitioning of the tower-based net CO₂ exchange in European grasslands into gross primary productivity and ecosystem respiration components using light response functions analysis. *Agriculture, Ecosystems and Environment* 121, 93-120.
- Graux, A.-I., Bellocchi, G., Lardy, R., Soussana, J.-F., 2013. Ensemble modelling of climate change risks and opportunities for managed grasslands in France. *Agricultural and Forest Meteorology* 170, 114-131.
- Graux, A.I., Lardy, R., Bellocchi, G., Soussana, J.-F., 2012. Global warming potential of French grassland-based dairy livestock systems under climate change. *Regional Environmental Change* 12, 751-763.

758 Herrero, M., Henderson, B. Havlík, P., Thornton, P.K., Conant, R.T., Smith, P., Wirsenius, S.,
 759 Hristov, A.N., Gerber, P., Gill, M., Butterbach-Bahl, K., Valin, H., Garnett, T., Stehfest,
 760 E., 2016. Greenhouse gas mitigation potentials in the livestock sector. *Nature Climate*
 761 *Change* 6, 452-461.

762 Hörtnagl, L., Barthel, M., Buchmann, N., Eugster, W., Butterbach-Bahl, K., Díaz-Pinés, E.,
 763 Zeeman, M., Klumpp, K., Kiese, R., Bahn, M., Hammerle, A., Lu, H., Ladreiter-Knauss,
 764 T., Burri, S., Merbold, L., 2018. Greenhouse gas fluxes over managed grasslands in
 765 Central Europe. *Global Change Biology*, doi:10.1111/gcb.14079

766 Holzworth, D.P., Huth, N.I., DeVoil, P.G., Zurcher, E.J., Herrmann, N.I., McLean, G., Chenu,
 767 K., van Oosterom, E.J., Snow, V., Murphy, C., Moore, A.D., Brown, H., Whish, J.P.M.,
 768 Verrall, S., Fainges, J., Bell, L.W., Peake, A.S., Poulton, P.L., Hochman, Z., Thorburn,
 769 P.J., Gaydon, D.S., Dalgliesh, N.P., Rodriguez, D., Cox, H., Chapman, S., Doherty, A.,
 770 Teixeira, E., Sharp, J., Cichota, R., Vogeler, I., Li, F.Y., Wang, E., Hammer, G.L.,
 771 Robertson, M.J., Dimes, J.P., Whitbread, A.M., Hunt, J., van Rees, H., McClelland, T.,
 772 Carberry, P.S., Hargreaves, J.N.G., MacLeod, N., McDonald, C., Harsdorf, J., Wedgwood,
 773 S., Keating, B.A., 2014. APSIM - Evolution towards a new generation of agricultural
 774 systems simulation. *Environmental Modelling & Software* 62, 327-350.

775 Huntzinger, D.N., Post, W.M., Wei, Y., Michalak, A.M., West, T.O., Jacobson, A.R., Baker,
 776 I.T., Chen, J.M., Davis, K.J., Hayes, D.J., Hoffman, F.M., Jain, A.K., Liu, S., McGuire,
 777 A.D., Neilson, R.P., Potter, C., Poulter, B., Price, D., Raczka, B.M., Tian, H.Q., Thornton,
 778 P., Tomelleri, E., Viovy, N., Xiao, J., Yuan, W., Zeng, N., Zhao, M., Cook, R. (2012)
 779 North American Carbon Program (NACP) regional interim synthesis: terrestrial biospheric
 780 model intercomparison. *Ecological Modelling* 232, 144-157.

781 Huth, N.I., Bristow, K.L., Verburg, K., 2012. SWIM3: Model use, calibration, and validation.
 782 *Transactions of the ASABE* 55, 1303-1313.

783 Imer, D., Merbold, L., Eugster, W., Buchmann, N., 2013. Temporal and spatial variations of
784 soil CO₂, CH₄ and N₂O fluxes at three differently managed grasslands. *Biogeosciences* 10,
785 5931-5945.

786 IPCC, 2006. N₂O emissions from managed soils, and CO₂ emissions from lime and urea
787 application. In: De Klein, C., Novoa, R.S.A., Ogle, S., Smith, K.A., Rochette, P., Wirth,
788 T.C., McConkey, B.G., Mosier, A., Rypdal, K. (eds.) Guidelines for national greenhouse
789 gas inventories. IGES, Japan, vol. 4, pp. 1-54. Available at [https://www.ipcc-](https://www.ipcc-nggip.iges.or.jp/public/2006gl/pdf/4_Volume4/V4_11_Ch11_N2O&CO2.pdf)
790 [nggip.iges.or.jp/public/2006gl/pdf/4_Volume4/V4_11_Ch11_N2O&CO2.pdf](https://www.ipcc-nggip.iges.or.jp/public/2006gl/pdf/4_Volume4/V4_11_Ch11_N2O&CO2.pdf) (access on
791 18 May 2018)

792 IPCC, 2013. Climate Change 2013: The physical science basis. Contribution of Working
793 Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change
794 [Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Doschung, J., Nauels, A.,
795 Xia, Y., Bex, V., Midgley, P.M. (eds.)]. IPCC, Geneva, Switzerland, 1535 pp.

796 IPCC, 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II
797 and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change
798 [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland,
799 151 pp.

800 Jones, J.W., Antle, J.M, Basso, B.O. et al., 2017a. Brief history of agricultural systems
801 modelling. *Agricultural Systems* 155, 240-254.

802 Jones, S.K., Helfter, C., Anderson, M., Coyle, M., Campbell, C., Famulari, D., Di Marco, C.,
803 van Dijk, N., Tang, Y.S., Topp, C.F.E., Kiese, R., Kindler, R., Siemens, J., Schrumpf, M.,
804 Kaiser, K., Nemitz, E., Levy, P.E., Rees, R.M., Sutton, M.A., Skiba, U.M., 2017b. The
805 nitrogen, carbon and greenhouse gas budget of a grazed, cut and fertilised temperate
806 grassland. *Biogeosciences* 14, 2069-2088.

807 Klumpp, K., Tallec, T., Guix, N., Soussana, J.-F., 2011. Long-term impacts of agricultural
808 practices and climatic variability on carbon storage in a permanent pasture. *Global Change*
809 *Biology* 17, 3534–3545.

810 Koncz, P., Pintér, K., Balogh, J., Papp, M., Hidy, D., Csintalan, Zs., Molnár, E., Szaniszló,
811 A., Kampfi, Gy., Horváth, L., Nagy, Z., 2017. Extensive grazing in contrast to mowing is
812 climate-friendly based on the farm-scale greenhouse gas balance. *Agriculture, Ecosystems*
813 *and Environment* 240, 121-134.

814 Kotteck, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World Map of the Köppen-
815 Geiger climate classification updated. *Meteorologische Zeitschrift* 15, 259-263.

816 Lanigan, G., Finn, J., Lüscher, A., 2013. Mitigation & adaptation options: grass-legume
817 mixtures. *AnimalChange* E-Newsletter,
818 <http://www.animalchange.eu/pdf/newsletter/nov2013.pdf>.

819 Li, F.Y., Snow, V.O., Holzworth, D.P., 2011. Modelling the seasonal and geographical
820 pattern of pasture production in New Zealand. *New Zealand Journal of Agricultural*
821 *Research* 54, 331-352.

822 Liebig, M.A., Gross, J.R., Kronberg, S.L., Hanson, J.D., Frank, A.B., Phillips, R.L., 2006.
823 Soil response to long-term grazing in the northern Great Plains of North America.
824 *Agriculture, Ecosystem and Environment* 115, 270-276.

825 Liebig, M.A., Gross, J.R., Kronberg, S.L., Phillips, R.L., Hanson, J.D., 2010. Grazing
826 management contributions to net global warming potential: a long-term evaluation in the
827 Northern Great Plains. *Journal of Environmental Quality* 39, 799-809.

828 Liebig, M.A., Kronberg, S.L., Hendrickson, J.R., Dong, X., Gross, J.R., 2013. Carbon dioxide
829 efflux from long-term grazing management systems in a semiarid region. *Agriculture,*
830 *Ecosystems and Environment*, 164, 137–144.

831 Lü, X.-T., Dijkstra, F.A., Kong, D.-L., Wang, Z.-W., Han, X.-G., 2014. Plant nitrogen uptake
 832 drives responses of productivity to nitrogen and water addition in a grassland. *Scientific*
 833 *Report* 4:4817, doi:10.1038/srep04817.

834 Ma, S., Lardy, R., Graux, A.-I., Ben Touhami, H., Klumpp, K., Martin, R., Bellocchi, G.,
 835 2015. Regional-scale analysis of carbon and water cycles on managed grassland systems.
 836 *Environment Modelling & Software* 72, 356-371.

837 Merbold, L., Eugster, W., Stieger, J., Zahniser, M., Nelson, D., Buchmann, N., 2014.
 838 Greenhouse gas budget (CO₂, CH₄ and N₂O) of intensively managed grassland following
 839 restoration. *Global Change Biology* 20, 1913-1928.

840 Newton, P.C.D., Lieffering, M., Bowatte, W.M.S.D., Brock, S.C., Hunt, C.L., Theobald,
 841 P.W., Ross, D.J., 2010. The rate of progression and stability of progressive nitrogen
 842 limitation at elevated atmospheric CO₂ in a grazed grassland over 11 years of Free Air CO₂
 843 enrichment. *Plant and Soil* 336, 433-441.

844 Newton, P.C.D., Lieffering, M., Parsons, A.J., Brock, S.C., Theobald, P.W., Hunt, C.L.,
 845 Theobald, P.W., Ross, D.J., 2014. Selective grazing modifies previously anticipated
 846 responses of plant community composition to elevated CO₂ in a temperate grassland.
 847 *Global Change Biology* 20, 158-169.

848 Oates, L.G., Jackson, R.D., 2014. Livestock management strategy affects net ecosystem
 849 carbon balance of subhumid pasture. *Rangeland Ecology & Management* 67, 19-29.

850 Parton, W.J., Hartman, M., Ojima, D., Schimel, D., 1998. DAYCENT and its land surface
 851 submodel: description and testing. *Global and Planetary Change* 19, 35-48.

852 Polley, H.W., Emmerich, W., Bradford, J.A., Sims, P.L., Johnson, D.A., Saliendra, N.Z.,
 853 Svejcar, T., Angell, R., Frank, A.B., Phillips, R.L., Snyder, K.A., Morgan, J.A., Sanabria,
 854 J., Mielnick, P.C., Dugas, W.A., 2010. Precipitation regulates the response of net

ecosystem CO₂ exchange to environmental variation on United States rangelands. Rangeland Ecology and Management 63, 176-186.

Probert, M.E., Dimes, J.P., Keating, B.A., Dalal, R.C., Strong, W.M., 1998. APSIM's water and nitrogen modules and simulation of the dynamics of water and nitrogen in fallow systems. Agricultural Systems 56, 1-28.

R Core Team, 2016. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>

Rees, R.M., Augustin, J., Alberti, G., Ball, B.C., Boeckx, P., Cantarel, A., Castaldi, S., Chirinda, N., Chojnicki, B., Giebels, M., Gordon, H., Grosz, B., Horvath, L., Juszczak, R., Klemedtsson, A.K., Klemedtsson, L., Medinets, S., Machon, A., Mapanda, F., Nyamangara, J., Olesen, J.E., Reay, D.S., Sanchez, L., Cobena, A.S., Smith, K.A., Sowerby, A., Sommer, M., Soussana, J.-F., Stenberg, M., Topp, C.F.E., Van Cleemput, O., Vallejo, A., Watson, C.A., Wuta, M., 2013. Nitrous oxide emissions from European agriculture - an analysis of variability and drivers of emissions from field experiments. Biogeosciences 10, 2671-2682.

Riedo, M., Grub, A., Rosset, M., Fuhrer, J., 1998. A Pasture Simulation Model for dry matter production, and fluxes of carbon, nitrogen, water and energy. Ecological Modelling 105, 141-183.

Rolinski, S., Müller, C., Heinke, J., Weindl, I., Biewald, A., Bodirsky, B.L., Bondeau, A., Boons-Prins, E.R., Bouwman, A.F., Leffelaar, P.A., te Roller, J.A., Schaphoff, S., Thonicke, K., 2018. Modeling vegetation and carbon dynamics of managed grasslands at the global scale with LPJmL 3.6. Geoscientific Model Development 11, 429-451.

Rosenzweig, C., Elliott, J., Deryng, D., Ruane, A.C., Müller, C., Arneth, A., Boote, K.J., Folberth, C., Glotter, M., Khabarov, N., Neumann, K., Piontek, F., Pugh, T.A., Schmid, E., Stehfest, E., Yang, H., Jones, J.W., 2014. Assessing agricultural risks of climate change in

the 21st century in a global gridded crop model intercomparison. Proceedings of the National Academy of Sciences 111, 3268-3273.

Ruane, A.C., Goldberg, R., Chryssanthacopoulos, J., 2015. Climate forcing datasets for agricultural modeling: Merged products for gap-filling and historical climate series estimation. *Agricultural and Forest Meteorology* 200, 233-248.

Sándor, R., Barcza, Z., Acutis, M., Doro, L., Hidy, D., Köchy, M., Minet, J., Lellei-Kovács, E., Ma, S., Perego, A., Rolinski, S., Ruget, F., Sanna, M., Seddaiu, G., Wu, L. Bellocchi, G., 2017. Multi-model simulation of soil temperature, soil water content and biomass in Euro-Mediterranean grasslands: Uncertainties and ensemble performance. *European Journal of Agronomy* 88, 22-40.

Sándor, R., Picon-Cochard, C., Martin, R., Louault, F., Klumpp, K., Borrás, D., Bellocchi, G., 2018. Plant acclimation to temperature: Developments in the Pasture Simulation model. *Field Crops Research*, doi:10.1016/j.fcr.2017.05.030.

Sándor, R., Barcza, Z., Hidy, D., Lellei-Kovács, E., Ma, S., Bellocchi, G., 2016. Modelling of grassland fluxes in Europe: Evaluation of two biogeochemical models. *Agriculture, Ecosystems and Environment* 215, 1-19.

Schulze, E.D., Luyssaert, S., Ciais, P., Freibauer, A., Janssens, I.A., Soussana, J.-F., Smith, P., Grace, J., Levin, I., Thiruchittampalam, B., Heimann, M., Dolman, A.J., Valentini, R., Bousquet, P., Peylin, P., Peters, W., Roedenbeck, C., Etiope, G., Vuichard, N., Wattenbach, M., Nabuurs, G.J., Poussi, Z., Nieschulze, J., Gash, J.H. and CarboEurope Team, 2009. Importance of methane and nitrous oxide for Europe's terrestrial greenhouse-gas balance. *Nature Geoscience* 2, 842-850.

Seijan, V., Lal, R., Lakritz, J., Ezeji, T., 2011. Measurement and prediction of enteric methane emission. *International Journal of Biometeorology* 55, 1-16.

904 Senapati, N., Jansson, P.E., Smith, P., Chabbi, A., 2016. Modelling heat, water and carbon
 905 fluxes in mown grassland under multi-objective and multi-criteria constraints.
 906 Environmental Modelling & Software 80, 201-224.

907 Senapati, N., Chabbi, A., Gastal, F., Smith, P., Mascher, N., Loubet, B., 2014. Net carbon
 908 storage measured in a mowed and grazed temperate sown grassland shows potential for
 909 carbon sequestration under grazed systems. Carbon Management 5, 131-144.

910 Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis,
 911 S., Lucht, W., Sykes, M.T., Thonicke, K., Venevsky, S., 2003. Evaluation of ecosystem
 912 dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global
 913 vegetation model. Global Change Biology 9, 161-185.

914 Skiba, U., Jones, S. K., Drewer, J., Helfter, C., Anderson, M., Dinsmore, K., McKenzie, R.,
 915 Nemitz, E., Sutton, M.A., 2013. Comparison of soil greenhouse gas fluxes from extensive
 916 and intensive grazing in a temperate maritime climate. Biogeosciences 10, 1231-1241.

917 Smith, P., Martino, D., Cai, Z., Gwary, D., Janzen, H.H., Kumar, P., McCarl, B., Ogle, S.,
 918 O'Mara, F., Rice, C., Scholes, R.J., Sirotenko, O., Howden, M., McAllister, T., Pan, G.,
 919 Romanenkov, V., Schneider, U., Towprayoon, S., Wattenbach, M., Smith, J.U. (2008)
 920 Greenhouse gas mitigation in agriculture. Philosophical Transactions of the Royal Society
 921 B: Biological Sciences 363, 789-813.

922 Smith, K.A., Thomson, P.E., Clayton, H., McTaggart, I.P., Conen, F., 1998. Effects of
 923 temperature, water content and nitrogen fertilisation on emissions of nitrous oxide by soils.
 924 Atmospheric Environment 32, 3301-3309.

925 Snow, V., Rotz, C.A., Moore, A.D., Martin-Clouaire, R., Johnson, I.R., Hutchings, N.J.,
 926 Eckard, R.J., 2014. The challenges - and some solutions - to process-based modelling of
 927 grazed agricultural systems. Environmental Modelling & Software 62, 420-436.

928 Soussana, J.-F., Allard, V., Pilegaard, K., Ambus, P., Amman, C., Campbell, C., Ceschia, E.,
929 Clifton-Brown, J., Czobel, S., Domingues, R., Flechard, C., Fuhrer, J., Hensen, A.,
930 Horvath, L., Jones, M., Kasper, G., Martin, C., Nagy, Z., Neftel, A., Raschi, A., Baronti,
931 S., Rees, R., Skiba, U., Stefani, P., Manca, G., Sutton, M., Tuba, Z., Valentini, R., 2007.
932 Full accounting of the greenhouse gas (CO₂, N₂O, CH₄) budget of nine European grassland
933 sites. *Agriculture, Ecosystems and Environment* 121, 121-134.

934 Soussana, J.-F., Barioni, L.G., Ben-Ari, T., Conant, R., Gerber, P., Havlik, P., Ickowicz, A.,
935 Howden, M., 2013. Managing grassland systems in a changing climate: the search for
936 practical solutions. In: 22nd International Grasslands Congress, 15-19 September, Sydney,
937 Australia, 18 p.

938 Soussana, J.-F., Klumpp, K., Ehrhardt, F., 2014. The role of grassland in mitigating climate
939 change. In: *Proceedings of EGF at 50: The future of European grasslands*, Grassland
940 Science in Europe 19, 75-87.

941 Soussana, J.-F., Pilegaard, K., Ambus, P., Berbigier, P., Ceschia, E., Clifton-Brown, J.,
942 Czobel, S., de Groot, T., Fuhrer, J., Horvath, L., Hensen, A., Jones, M., Kasper, G., Martin,
943 C., Milford, C., Nagy, Z., Neftel, A., Raschi, A., Rees, R.M., Skiba, U., Stefani, P., Saletes,
944 S., Sutton, M.A., Tuba, Z., Weidinger, T., 2004. Annual greenhouse gas balance of
945 European grasslands - first results from the GreenGrass project. In: *International*
946 *conference greenhouse gas emissions from agriculture-mitigation options and strategies*,
947 10-12 February, Leipzig, Germany, pp. 25-30.

948 Soussana, J.-F., Tallec, T., Blanfort, V., 2010. Mitigating the greenhouse gas balance of
949 ruminant production systems through carbon sequestration in grasslands. *Animal* 4, 334-
950 350.

951 Tubiello, F., Salvatore, M., C ndor Golec, R., Ferrara, A., Rossi, S., Biancalani, R., Federici,
952 S., Jacobs, H., Flammini, A., 2014. Agriculture, forestry and other land use emissions by

953 sources and removals by sinks 1999-2011 analysis, Working Paper Series ESS/14-02, FAO
 954 Statistical Division, Rome, Italy. Available at:
 955 <http://www.fao.org/docrep/019/i3671e/i3671e.pdf> (access on 15 May 2018)

956 Valin, H., Havlik, P., Mosnier, A., Herrero, M., Schmid, E., Obersteiner, M., 2013.
 957 Agricultural productivity and greenhouse gas emissions: trade-offs or synergies between
 958 mitigation and food security? *Environmental Research Letters*, 8, 035019.

959 Van Groenigen, J.W., Velthof, G.L., Oenema, O., Van Groenigen, K.J., Van Kessel, C., 2010.
 960 Towards an agronomic assessment of N₂O emissions: a case study for arable crops.
 961 *European Journal of Soil Science* 61, 903-913.

962 Venterea, R.T., Bijesh, M., Dolan, M.S., 2011. Fertilizer source and tillage effects on yield-
 963 scaled nitrous oxide emissions in a corn cropping system. *Journal of Environmental*
 964 *Quality* 40, 1521-1531.

965 UK Rural Payments Agency, 2003. Cattle scheme literature: Notes for guidance 2003. The
 966 Rural Payments Agency of the UK Department for Environment, Food and Rural Affairs
 967 (through <https://www.gov.uk/government/organisations/rural-payments-agency>).

968 Warszawski, L., Frieler, K., Huber, V., Piontek, F., Serdeczny, O., Schewe, J., 2014. The
 969 Inter-Sectoral Impact Model Intercomparison Project (ISI-MIP): project framework.
 970 *Proceedings of the National Academy of Sciences of the United States of America* 111,
 971 3228-3232.

972 West, T.O., Marland, G., 2002. A synthesis of carbon sequestration, carbon emissions, and net
 973 carbon flux in agriculture: comparing tillage practices in the United States. *Agriculture,*
 974 *Ecosystems and Environment* 91, 217-232.

975 White, T.A., Johnson, I.R., Snow, V.O., 2008. Comparison of outputs of a biophysical
 976 simulation model for pasture growth and composition with measured data under dryland
 977 and irrigated conditions in New Zealand. *Grass and Forage Science* 63, 339-349.

978 Wu, L., McGechan, M.B., McRoberts, N., Baddeley, J.A., Watson, C.A., 2007. SPACSYS:
 979 Integration of a 3D root architecture component to carbon, nitrogen and water cycling-
 980 Model description. *Ecological Modelling* 200, 343-359.

981 Wu, L., Rees, R.M., Tarsitano, D., Zhang, X., Jones, S.K., Whitmore, A.P., 2015. Simulation
 982 of nitrous oxide emissions at field scale using the SPACSYS model. *Science of the Total*
 983 *Environment* 530-531, 76-86.

984 Yuan Z.Y., Li, L.H., Han, X.G., Chen, S.P., Wang, Z.W., Chen, Q.S., Bai, W.M., 2006.
 985 Nitrogen response efficiency increased monotonically with decreasing soil resource
 986 availability: a case study from a semiarid grassland in northern China. *Oecologia* 148, 564-
 987 572.

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